

Environments and molluscs in a non – calcareous forest area in southern Sweden

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ENVIRONMENTS AND MOLLUSCS IN A NON-CALCAREOUS

FOREST AREA IN SOUTHERN SWEDEN

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Title and subtitle
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Abstract
Environments and mollusc faunas were investigated in oligotrophic spruce and oak forests and in herb-rich deciduous woods. The latter habitat had a much richer fauna. Correlations with calcium in litter and with soil moisture were found.

Cochlicopa lubrica (Müll.) has a small annual number of juveniles. Reproduction occurs in summer and autumn in southern Sweden. By rearing it was shown that calcium citrate, calcium oxalate and sodium carbonate had positive effects on the reproductive output. *Discus rotundatus* (Müll.) was also studied with similar results. Ca citrate, common in leaves of nutrient-demanding trees, was better for the snails than Ca oxalate, which is probably not utilized until it has been broken down by microorganisms. Calcium is to great extent oxalate-bound in spruce and oak forests. It is inferred from the Na_2CO_3 experiments that pH per se may have an effect on reproduction at low calcium levels.

Changes in food preferences were observed in laboratory experiments, when two species were introduced in the same test chamber. On more calcium-rich litter the competitive interactions seemed to decrease.

A group of species correlated with low calcium content was found in the herb-rich woods. These species occur in other parts of Sweden in calcium-rich habitats. Some other snail species with a wide ecological amplitude were common at sun-exposed localities in the herb-rich woods, probably because of decreased competition pressure there. Contrary to prevailing opinions, it is considered that interspecific food competition may be important for woodland molluscs.

Key words
Environments, mollusc faunas, forests, calcium, moisture, rearing, *Cochlicopa lubrica*, *Discus rotundatus*, calcium citrate, calcium oxalate, reproductive output, pH per se, food preferences, competitive interactions.

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LIST OF PAPERS

This thesis is based on the following papers:

- A. Wäreborn, I. 1969. Land molluscs and their environments in an oligotrophic area in southern Sweden. - Oikos 20: 461-479. Reprinted by kind permission of Oikos.
- B. Wäreborn, I. On the life history of Cochlicopa lubrica (Müll.): a biometrical study. Manuscript.
- C. Wäreborn, I. Reproductive success of two species of land snails in relation to calcium salts in forest litter. Manuscript.
- D. Wäreborn, I. Food preferences and competition among some species of woodland snails. Manuscript.
- E. Wäreborn, I. Environments and molluscs in a non-calcareous forest area in southern Sweden; with remarks on competition among terrestrial snails. Manuscript.

In the following paper A will be referred as Wäreborn 1969 and papers B - E by their respective letters.



INTRODUCTION

Although living plant tissues to some extent are eaten by terrestrial molluscs, most species feed mainly on dead plant material (Mason 1970, Jennings and Barkham 1975). Fungi are also consumed, and bacteria may be a more or less important addition to the food (Fog 1979). Food preferences of woodland mollusc species are largely unknown. In laboratory experiments with Cepaea nemoralis L. (Grime et al. 1978) the animals showed a rather selective feeding, avoiding plant material with hard surfaces. Detering substances in plants were also demonstrated. Effects of food competition among woodland molluscs were rejected by Boycott (1934) and Waldén (1981), but are indicated in a few cases (Harvey 1974, Cameron 1978, Carter et al. 1979).

Molluscs probably have less importance quantitatively than earthworms for the leaf litter decomposition in most habitats (Lindquist 1941, Frömming 1958, Mason 1971, Jennings and Barkham 1979). About 1 - 17 % of the leaf litter production in different forest types may be consumed.

Snails may assimilate about 50 % of the weight of ingested leaf litter (Mason 1970), which is a comparatively high proportion. According to Nielsen (1962), molluscs have a very complete system of digestive enzymes. e.g. chitinases, cellulases, pectinases and xylanases. They also have peroxidases (Neuhausser and Hartenstein 1978), able to remove certain chemical groups from the lignin molecules; the remains are slowly transformed into humus. There may be interspecific differences in intestinal enzyme production (Marcuzzi and Turchetto Lafisca 1975).

The slime of the molluscs may contain almost half their organic production (Richardson 1975). This might be important for soil microorganisms in some habitats.

Predators on terrestrial molluscs include birds, especially thrushes (Richards 1977), hedgehogs (Demelow 1963), shrews (Frömming 1954), some rodents (Parisi and Gandolfi 1974), beetles, e.g. the glow-worm Lampyris noctiluca (L.), and many species of parasitic flies (Baronio 1975).

In connection with egg laying birds consume snail shells to supply their requirements of calcium (Schifferli 1977). Empty shells may be very common in some forest habitats (cf. Mason 1974). Snails are often found eating on such shells. On hard surfaces of calcium carbonate they show a special etching behaviour

(Kühnelt 1932, Schmidt 1955); it was shown that snails may assimilate calcium through the sole (Kado 1960).

Relations between molluscs and the element of calcium were the object of a great number of studies (Peake 1978:480), but few of them dealt with the calcium factor in calcium-poor habitats (Bishop 1980). As the environmental variables are to a great extent interwoven, the importance of calcium cannot be studied in isolation. Differences in vegetation, decomposition of litter, pH values and several other variables are correlated with calcium content in the habitat. The element occurs in plant material in various chemical forms, that may affect soil animals differently.

Another important complex of variables, interacting with the previous ones, comprises soil moisture, air humidity and sun exposure (cf. Hagen 1952).

A FIELD STUDY OF LAND MOLLUSCS AND THEIR ENVIRONMENTS

(Wäreborn 1969)

The investigation was carried out in a mainly oligotrophic inland forest area in the southern part of the province of Småland, earlier studied faunistically by Lohmander (1953, 1954).

The mollusc faunas and the environmental conditions were investigated in five locality series, placed in four types of forest vegetation, later reclassified according to Nordiska Ministerrådet 1980: 1. moist oligotrophic mixed wood (= spruce forest of wet dwarf-scrub-type), 2. drier oligotrophic mixed wood (= spruce forest of Vaccinium myrtillus type), 3. oligotrophic oak wood (= oak forest of herb-poor type), and 4. meadow wood (= mixed broad leaved forest of herb-rich type). As the localities in the latter forest type were divided into a dry and a moist series on the basis of soil moisture, there were five locality series corresponding to five types of mollusc habitats.

Calcium content, soil acidity, thickness of soil layers and partly also soil moisture were measured, while other variables were estimated. Correlations were found between calcium contents in the litter and snail abundance in two of the oligotrophic locality series and between soil moisture and snail abundance in one of the relatively eutrophic (= meadow wood) series. The mollusc faunas differed considerably between oligotrophic and eutro-

phic forest types. Only one species was, however, restricted to the oligotrophic habitats.

As the litter is much richer in calcium than the underlying mineral soil, it is important to analyse the former material, when performing mollusc studies in non-calcareous forest areas.

The study indicated that mollusc fauna differences might be related to differences in the chemical form of the litter calcium. The calcium oxalate in oak and beech leaves and the more soluble calcium salts in leaves of ash, lime, maple and elm seemed to have different effects on the soil pH.

ON THE LIFE HISTORY OF COCHLICOPA LUBRICA (MÜLL.), PAPER B

As C.lubrica was chosen for rearing experiments, the naturally occurring reproduction period and the number of juveniles per adult snail were of interest. Eight sift collections from southern Sweden were studied biometrically, and with the aid of winter lines in the shells it was possible to place the juveniles into year classes. The reproductive output under natural conditions was found to be low: 1 - 14 juveniles per adult snail per year. The season of reproduction comprised the summer and the autumn in southern Sweden. The juveniles need about 2.4 - 3.5 years to reach adult stage. The results were compared with information on C.lubrica in England and Poland.

ON REPRODUCTIVE SUCCESS OF REARED COCHLICOPA LUBRICA AND DISCUS ROTUNDATUS (MÜLL.), PAPER C

Substantial increases in reproductive output of the two species studied were obtained with calcium citrate and calcium oxalate additions to the leaf litter substrate. The former calcium salt was more favourable for the snails. A small but significant increase in juvenile numbers was obtained, when pH was raised with sodium carbonate. Calcium oxalate is probably not utilized by the snails until it has been broken down by microorganisms in the litter. Calcium and pH changes may be correlated with differences in microorganism occurrence on the leaf surfaces. Snails may partly but probably do not mainly feed on microorganisms. The increase in reproductive output of the two species at the relatively low initial calcium and pH levels used in the experi-

ments is ascribed to the increase of available calcium and partly also to the raised pH. Differences in microorganism growth might contribute to the increase of juvenile numbers.

It is inferred from the results that the low abundance or the absence of C.lubrica and D.rotundatus in oligotrophic habitats in the study area to great extent is due to low calcium content and low pH values. The role of the calcium oxalate in forest ecosystems in relation to mollusc distribution is discussed.

FOOD PREFERENCES AND COMPETITION AMONG SOME SPECIES OF WOODLAND SNAILS (PAPER D)

In preference experiments some species reacted positively to calcium citrate and to high pH, while others were indifferent. No reactions to calcium oxalate were obtained. This calcium compound, predominating in nutrient-poor habitats, has no direct effect upon pH. Mollusc slime has a high pH, due to a high calcium content. The animals are thus to some extent able to neutralize acid substances.

When tested in single species experiments on a relatively calcium-poor leaf litter, most of the snail species preferred lime leaves to leaves of oak and hornbeam. Significant changes in preference, indicating a partial niche differentiation, were obtained when two species were introduced in the same test chamber.

Competitive interactions decreased, when the species were kept on a diet of leaf litter from a more calcium-rich locality. In late summer, when the amount of leaf litter from nutrient-rich tree species, e.g. lime, decreases on the woodland floor, the competition pressure may be critical for some species.

A FURTHER ANALYSIS OF THE FIELD STUDY (PAPER E)

A more consistent picture of the role of calcium in the mollusc environment was obtained by calculating calcium as per mille of ash-free dry weight of the analysed material according to Sjörs (1971). The change relative to Wäreborn 1969 was greatest in the herb-rich deciduous woods, which in relation to the organic content of the analysed material have a much higher calcium content than the oligotrophic oak woods.

The connections in the three oligotrophic habitats between snail abundance and calcium and between number of mollusc species and calcium are corroborated by this study.

Based on snail fauna similarities three locality groups were discerned in the herb-rich deciduous woods (Wäreborn 1969). Group I was found to be shady and relatively calcium-poor, group II was sun-exposed and group III shady and calcium-rich. A number of species characteristic of the relatively calcium-poor locality group I occur in other parts of Sweden in very calcium-rich habitats. Some species with a wide ecological amplitude show an increased abundance at the localities in group II, probably because of a decreased competition pressure there from drought-sensitive species.

The results of this study, together with those presented in paper D, indicate that interspecific food competition occurs between molluscs under natural conditions during critical periods of the year.

CONCLUSIONS

The existing pattern of occurrence of woodland molluscs in non-calcareous areas of southern Sweden seems to be best explained as effects of the following environmental variables:

- a) plant species composition: there are great differences between various kinds of forest habitats with their different litter decomposition (mor, moder and mull types of humus);
- b) soil moisture: this seems to be limiting at localities in the drier, herb-rich deciduous woods;
- c) sun exposure: differences between sheltered and exposed localities are probably important in the two herb-rich deciduous wood series; in exposed localities there will be periods of low relative humidity in the micro-habitats of the molluscs;
- d) total calcium content in the litter;
- e) distribution of calcium between oxalate-bound form and other forms of occurrence;
- f) soil acidity, which is related to the preceding two points and to point a;
- g) interspecific competition; and

h) human interference (e.g. spruce plantations replacing deciduous wood).

Differences in snail distribution related to calcium content in litter have been observed also among species characteristic of the herb-rich deciduous wood habitat. It is made probable that, contrary to prevailing opinions, food competition plays a role among woodland molluscs in critical periods of the year.

Land snails appear to be sensitive to acidification and calcium leaching (cf. paper C). Therefore they seem to be suitable objects for studies of human interferences in nature.

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Land molluscs and their environments in an oligotrophic area in southern Sweden

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Abstract

Environmental factors influencing the occurrence of land molluscs (calcium, pH, moisture, vegetation) were studied in five types of woodland habitat, chosen in a CaCO_3 -free area. The necessary supply of Ca occurs in organic material, mainly in litter and foena. Correlations between the Ca content in the foena and abundance of snails were found and also between Ca and number of mollusc species. Different Ca salts dominate in the leaves of different tree species. The relatively high content of Ca oxalate at most oak wood localities has no direct pH increasing effect, while there is a pH increase in the soil surface at localities with ash, lime, maple and elm, probably depending upon the fact that in litter from these trees more soluble and therefore more alkaline Ca salts, e.g. Ca citrate, dominate. Forests containing the latter tree species often have rich mollusc faunas. Correlations between soil moisture and abundance of snails were also found.

Резюме

Были исследованы факторы окружающей среды (наличие кальция, pH, растительности, степень сырости), влияющие на существование земельных (сухопутных) слизняков.

Для исследования были выбраны 5 типов »Woodland Habitat« из окружающей местности без наличия CaCO_3 .

Необходимое снабжение кальцием происходит посредством органических веществ, находящихся, главным образом, в помете, гнилой листве и хвое.

Было установлено соотношение между листвою и хвоею, содержащих кальций, и наличия члеников.

Различные соли кальция преобладают в листве разных типов деревьев.

Оксалат кальция, а также и легко растворимые соли кальция, напр. щавелевокислый кальций (цитратнокислый кальций), очевидно влияет на слизняков в многих отношениях.

Было также установлено соотношение между степенью сырости земли и наличия члеников.

1. Introduction

Calcium may in nature be present in bedrock and soil as calcite (CaCO_3). Molluscs are able to assimilate CaCO_3 (Schmidt 1955, Voelker 1959); the Ca- and CO_3 -ions are utilized to build the shell (Blumberger 1959). In other areas this mineral is absent. By erosion of the silicate bedrock there, Ca ions are slowly released and eventually becoming incorporated in the organic material of the woodland floor, mainly as salts of organic acids. Field studies have shown that many mollusc species live in habitats, where there is no CaCO_3 (cf. Boycott 1934, Ložek 1962). Such species have been characterized as indifferent to the bedrock type. In some cases, however, a positive effect from greenstone rocks has been demonstrated (Lundgren 1954, Lohmander 1953).

The present investigation aimed at examining the mollusc fauna and its relation to environmental factors, particularly Ca, in five different forest habitats in southern Sweden. Three of the habitats are oligotrophic: moist mixed wood, drier mixed wood and oak wood, and two are meso-eutrophic deciduous forests: dry meadow wood and moist meadow wood. About 75 localities were studied.

The nomenclature follows Zilch and Jaekel (1962) and Waldén (1966 a, 1966 b).

2. Study area

Field studies were carried out in the summers 1963–67 in an area of about 40×50 km in the southern part of the province of Småland (Fig. 1). It is mainly oligotrophic. Ground with better soil has as a rule been cultivated. Through the area from Målaskog (D45) in the north to Almås (E45) in the south runs a narrow, intermittent course of greenstone ridges. It consists of alkaline rocks, mostly hyperite. On both sides of the course to a distance of up to 20 km there are smaller outcrops of the same (or similar) bedrock. The total greenstone area is only a few km^2 .

The main part of the study area lies on

ferroferrous gneiss. Bedrocks and moraines containing CaCO_3 are absent.

Woods on gneiss are as a rule of a coniferous heath type. The blueberry-spruce wood is the most widespread plant community. Large tracts are covered with moist oligotrophic woodland. On stony, hilly ground, mainly close to human settlements, oak wood occurs. Deciduous wood rich in herbs is rare, mainly being restricted to the slopes of the greenstone ridges. The flora of the province is described by Hård av Segerstad (1924).

No large local differences in climate occur in the area. Precipitation is moderate (600–800 mm/year). The number of days with ≥ 1 mm is on the average 110–120 per year. The summers of 1963, 1964 and 1965 were more rainy than the average. The early summer in 1966 was dry and during 1967 there were several spells of dry weather.

3. Methods

For quantitative sampling a combination of a square method ("squares" about 10×20 m) and a volume method was chosen (cf. Balogh 1958: 342–343). Collecting was done by sifting moss, litter, foerna, etc., by hand-picking and by shaking the vegetation. It was not possible to sift all material in the large squares; it was tried by selection from different parts of the habitat to make the sample representative of the square. The volume after sifting was 2.9–4.5 l (average 3.5 l). The number of snails obtained has then been evaluated to correspond to 3.0 l. The squares were chosen to be as uniform as possible. Collecting was carried out from the middle of June to the end of August.

When the sample was dry the snails were removed by hand under a magnifying glass.

The composition of the plant community, the slope and moisture of the ground, the shading, the occurrence of litter and foerna and signs of human activity were noted. A soil profile, dug to a depth of about 50 cm,

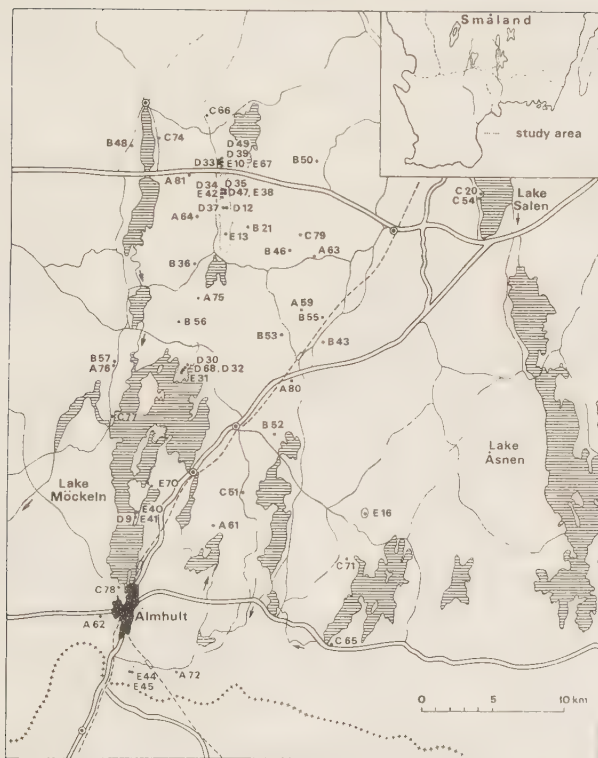


Fig. 1. Study area (1:400000). A. Localities in the moist mixed wood series, B. the drier mixed wood series, C. the oak wood series, D. the dry meadow wood series and E. the moist meadow wood series.

was examined. pH was measured colorimetrically at the surface and at a depth of about 10 cm (S.K.P. Soil Tester, Weibull Ltd.; cf. Steubing 1965: 179). The values obtained deviate at most by 0.25 units from those determined with a standard glass electrode. In soil profiles with distinct horizons, pH was measured in each of them. Soil samples were taken

at a depth of 5–15 cm and in podzol profiles in the leached zone. In the moist mixed wood series, however, this zone was mostly very deep down, so here the corresponding samples consist of peat or peat-mould.

Weighed amounts (two parallel tests) of sifted material or of soil samples (air-dried) were ashed and extracted with hot 7.5 M HCl.

Ca analyses were performed on the extracts (Standard 1950: 8 from The Royal Swed. Agric. Board). The method yields all Ca in the analysed matter except that combined with silicates.

The sifted samples give the mean calcium content in the foena layer. Newly fallen leaves rarely pass through the sieve and are thus not represented in the material.

Occurrence of carbonate was tested with HCl (with CaCO_3 CO_2 is obtained and measured in a gas buret).

The moisture condition of the ground was subjectively estimated or measured by the carbide method (Steubing 1965: 100). Sampling for this test was made at all meadow wood localities simultaneously (18.8.1966 at 13.30–14.12 hrs.). Three samples of the upper earth layer down to a depth of 3 cm were taken at each locality: one relatively far down the slope, one approximately in the middle and one at the upper end. The day of the test was preceded by three days of fine weather.

At two localities temperature and relative humidity (RH) were measured by a thermistorized aspiration psychrometer (Hygrophil, Ultrakust Gerätebau, W. Germany).

4. General results of the soil investigation

In the parallel Ca analyses of sifted foena, an average difference of 0.43 mg/g was obtained; $s = 0.27$. Corresponding values for parallel soil analyses were 0.23; $s = 0.15$. If $p \leq 0.01$, $x \pm 0.57$ mg/g is obtained for the sifted material and $x \pm 0.31$ mg/g for the soil samples. The greater variation in the sifted samples is a result of their lower homogeneity. When the differences are relatively great, the higher value of Ca content almost always corresponds to a higher value of organic content.

No correlation was found between the Ca contents of foena and of underlying layers (Fig. 2). The foena was always much richer in Ca (cf. Linnermark 1960). The difference was greatest in the oak wood series.

In spite of the relatively high Ca content in some of the mineral soil samples from the meadow wood series it was not possible to

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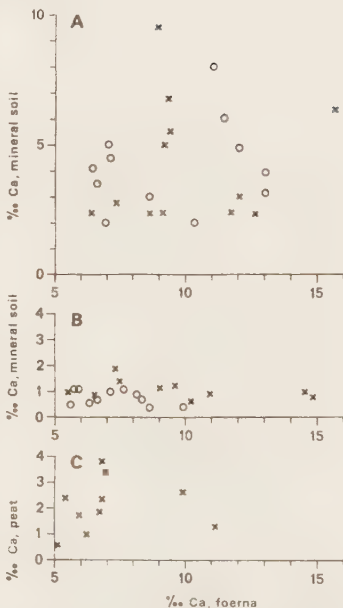


Fig. 2. Calcium contents in foena (sifted material) and in soil samples. A. The meadow wood series: $\circ$ = the dry meadow wood series, $\times$ = the moist meadow wood series. B. The oak wood series ($\times$) and the drier mixed wood series ($\circ$). C. The moist mixed wood series.

prove presence of CaCO_3 (cf. Valovirta 1968). Probably calcium is partly dissolved from more easily weathered greenstone minerals by HCl in the analysis. Actually 0.001 M HCl dissolves some calcium from hyperite and at increasing HCl concentration the solubility increases (J. Nilsson, unpubl.). The shells of dead snails, carefully picked away before the analyses, constitute for the molluscs a CaCO_3 source of unknown importance.

The relation between Ca content and pH is rather indefinite (Fig. 3; cf. Ant 1963). The variation of pH within a seemingly uniform

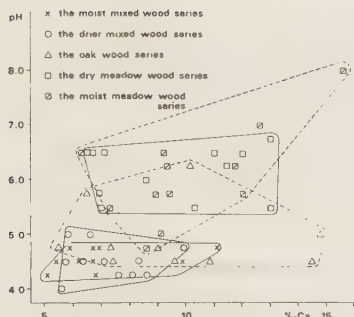


Fig. 3. The pH of the soil surface in relation to Ca contents of the foena.

test area may amount to one pH unit or even more. Ant found a seasonal variation of the same order. During the summer however, the values are rather stable. The mean value at the soil surface is approximately equal to that at about -10 cm in the oligotrophic series, while pH in the meadow wood series is about one unit higher at the surface. The meadow wood vegetation with its foena of leaves from deciduous trees gives high pH values in the upper layer of the mineral soil, but it becomes rapidly more acid downwards. In foenas of oak (and beech) Ca occurs mainly in the form

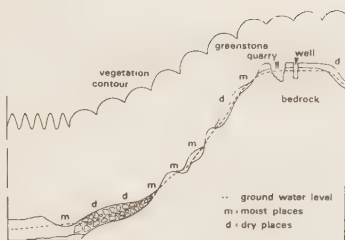


Fig. 4. Profile of a greenstone ridge showing the distribution of moisture.

of oxalate (Mattson and Koutler-Andersson 1946, Linnermark 1960). This salt is difficult to dissolve and has no (or almost no) effect upon the pH. In leaves of ash and probably also lime, maple and elm most Ca salts are easily dissolved and decidedly alkaline, e.g. calcium citrate. This might cause the high pH in the soil surface at the meadow wood localities.

The ground water level is high in the greenstone ridges in the area and moist ground may occur high up on steep slopes. At the foot of the slopes there is often rocky ground with thick organic layers. Such ground is often well-drained, and under the foena low soil moisture values are found (Fig. 4).

Temperature and RH showed a rather

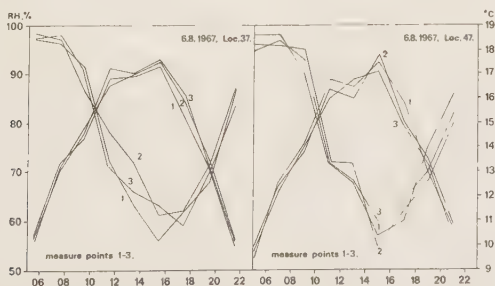


Fig. 5. Temperature and RH. Measuring was done during a sunny and windy day (wind about 8 m/sec. from NW). Loc. 37 had a lower soil moisture, but it was more shaded and sheltered against wind.

small variation in the studied localities (Fig. 5). RH is influenced by soil moisture and by shading (Hagen 1952).

5. The habitats and their mollusc fauna

The five habitat types examined may be characterized as follows:

1. Moist, oligotrophic mixed wood with *Vaccinium*, *Sphagnum* spp. and *Polytrichum commune* L.

2. Mixed coniferous wood with birches, medium soil moisture and in the undergrowth *Vaccinium myrtillus* L.

3. Oak wood with *V. myrtillus*, *Deschampsia flexuosa* (L.) and other heath plants.

4. Meadow wood on relatively dry ground on rocky hillsides containing deciduous trees, e.g. lime, ash, maple and elm together with oak and birch. Herbs and grass occur. *Vaccinium* spp. and other heath plants are absent.

5. As type 4, but with greater soil moisture.

Further data are presented below. The mollusc species found are listed according to their constancy and dominance values. On calculating the constancy dead shells were included.

Interspecific competition may interfere with environmental factors, but amongst terrestrial mollusc species it seems to be unimportant (Boycott 1934). Species of oligotrophic habitats are generally present at more favourable localities and are there as a rule more abundant, in spite of the several other species also present. The supply of food is usually very good, even if towards the end of the season the amount of leaves from lime, ash, maple and elm considerably decreases in the forest. In view of the weak competition, dominance values ought to be looked upon only as a representation of the percental composition of the fauna. One of the species (*Oxychilus alliarius* Mill.) is, however, carnivorous and attacks other mollusc species.

Catching slugs is weather-dependent and these are probably underrepresented in the material. The seemingly very poor slug fauna

of the moist oligotrophic forests possibly depends on the dry and sunny weather at the time of the sampling. *Arion subfuscus* (Drap.) and *Limax tenellus* (Müll.) are known to be very common in oligotrophic habitats in the area (Lohmander 1953, 1954). The latter species is not fully developed until the autumn. *Vitrina pellucida* (Müll.) has its main activity period in spring and autumn and may also be underrepresented.

5.1. The moist, oligotrophic, mixed wood series

Ten localities were investigated (series A, Fig. 1). Habitat data are given in Tab. 1. The ground was approximately level. Downwards, the peat might change into peat-mould or into a distinct, leached zone.

A											
Loc.											
No.	81	59	72	64	76	63	61	75	62	80	B
											Loc.
	80	76	63	74	81	82	80	80	71	80	No.
	62	73	63	78	79	81	88	88	84		48
	75	62	59	68	75	83	85	92			57
	61	67	63	73	76	82	89			94	52
	63	76	71	81	84	89			96	91	43
	76	78	72	79	83			89	91	87	46
	64	80	79	89			93	92	89	83	55
	72	83	84			84	79	88	82	79	36
	59	77			90	87	82	87	81	77	56
	81			60	61	54	57	59	57	57	50
				58	73	77	63	58	67	61	58
				28	16	30	25	23	16	24	18
											12
											10
											53
Loc.											
No.	53	21	50	56	36	55	46	43	52	57	48
C											
Loc.											
No.	54	74	77	20	79	78	66	65	51	71	
	71	60	56	70	67	61	53	55	69	81	
	51	78	72	78	80	70	61	66	81		
	65	71	69	74	84	81	75	79			
	66	70	64	72	82	81	81				
	78	80	68	80	80	90					
	79	81	74	87	88						
	20	81	76	86							
	77	84	80								
	74	85									
	54										

Fig. 6. Dominant identity between different localities. A. The moist mixed wood series. B. The drier mixed wood series. C. The oak wood series. The highest values of dominant identity have been marked with fat numbers or italics.

Tab. 1. Environmental conditions in the moist mixed wood series. The localities are arranged according to increasing Ca content in the foena. Explanation of symbols: 1 = sparse, 2 = relatively abundant, 3 = dominating (for leaf litter & foena and wood litter: 3 = very abundant); light conditions: 1-5 (1 = very shady, 5 = very exposed); peat layer: + = downwards changing into mould.

Habitat characteristics	Locality No.										
	61	75	62	63	80	81	76	64	72	59	Average
Deciduous trees											
<i>Betula</i> , <i>Salix</i> , etc.	3	2	2	2*	2	2	2	2	2	2	
<i>Alnus glutinosa</i> (L.)	-	1	-	1	-	1	1	-	-	-	
Coniferous trees											
<i>Picea abies</i> (L.)	1	2	2	2	2	3	2	3	2	2	
<i>Pinus silvestris</i> L.	2	1	1	1	1	1	1	1	1	1	
Indicators of soil moisture											
<i>Sphagnum</i> spp.	2	3	3	3	3	1	3	3	3	3	
<i>Polytrichum commune</i>	2	2	3	2	1	3	1	2	3	2	
Others (<i>Rubus chamaemorus</i> L., <i>Juncus effusus</i> L., etc.)	1	1	1	1	1	2	-	2	2	1	
Oligotrophic plants											
<i>Vaccinium myrtillus</i> and <i>V. vitis idaea</i> L.	1	1	2	2	1	2	2	1	2	1	
<i>V. uliginosum</i> L.	2	-	-	-	-	-	-	2	-	1	
<i>Deschampsia flexuosa</i> , etc.	1	1	-	1	1	-	1	-	1	1	
Mesotrophic plants											
(<i>Oxalis</i> , etc.)	1	-	1	1	1	1	1	-	1	-	
Light conditions	3	2	4	3	3	2-3	3	4	4	3	
Leaf litter & foena	1	1	1	1	1	2	1	1	2	2	
Abundance of wood litter	2	1	2	1	1	1	1	1	3	1	
Thickness of peat layer, cm	>35*	40	30*	33*	>40*	>45*	>40*	>37*	>15	13	
Ground water surface at cm	-	-	-	-	-	-	-	40	27	-	
Ca, %											
in the foena	5.1	5.4	5.9	6.2	6.7	6.7	6.8	6.9	9.9	11.1	7.1
in the peat layer (at a depth of 5-15 cm)	0.6	2.4	1.7	1.0	1.9	3.8	2.4	3.4	2.6	1.3	2.1
pH											
in surface layer of soil	4.3	4.5	4.8	4.5	4.5	4.8	4.3	4.8	4.5	4.8	4.6
at a depth of about 10 cm	4.5	4.5	4.5	4.5	4.3	4.3	4.5	5.0	4.5	4.5	4.5

* no *Salix* spp.

The mollusc fauna is presented in Tab. 2. On the basis of the dominance values, which are given as a mean for each species, dominant identity according to Renkonen (1938) was calculated for all locality combinations. Thereby the localities were compared in pairs. For each species the lowest dominance value was chosen and added to give the dominant identity between the two localities (Fig. 6). This and the resemblance in species composition show that the series is very homogeneous. Ca content and individual numbers show a good correlation (Fig. 7).

Some exceptions from expected values occurred. Locality 61 had a low Ca content but

a high individual number, probably because of a richer supply of birch foena. Locality 72 had a relatively high Ca content, but the high ground water level may have given unfavourable conditions. Recent ditching near locality 80 had probably lowered the water level.

5.2. The drier mixed wood series

Eleven localities were investigated (series B, Fig. 1). Areas containing *Sphagnum* spp. were avoided. Habitat data are given in Tab. 3.

The mollusc fauna is presented in Tab. 4 and the dominant identity in Fig. 6. There is a tendency towards a higher individual number at localities rich in Ca. Statistically signif-

Tab. 2. The mollusc fauna of the moist mixed wood series. The individual numbers are recalculated to correspond to a sample volume of 3 l. MI = mean number of individuals/locality. C = constancy. Dm = dominance value, average for the species. I = few individuals only, II = abundant. + = found on a second visit to the locality. The localities are arranged according to increasing Ca content in the foena.

Species	Locality No.											Mi	C %	Dm
	61	75	62	63	80	81	76	64	72	59				
<i>Nesovitrea hammonis</i>	79	22	27	38	7	32	21	15	32	96	36.9	100	65.2	
<i>Euconulus f. fulvus</i>	9	3	4	9	1	13	5	6	16	78	14.4	100	18.2	
<i>Columella aspera</i>	5	+	3	3	2	6	1	3	4	13	4.0	100	7.1	
<i>Vertigo substriata</i>	3	—	—	2	2	7	3	1	3	10	3.1	80	5.1	
<i>Oxychilus alliarius</i>	—	1	—	—	—	1	2	—	2	0.6	40	1.6		
<i>Clausilia bidentata</i>	—	—	2	—	—	2	—	—	3	—	0.7	30	1.1	
<i>Punctum pygmaeum</i>	—	—	—	—	—	1	1	—	—	12	1.4	30	1.0	
<i>Discus ruderratus</i>	—	—	1	—	—	5	—	—	—	—	0.6	20	0.9	
<i>Cochlicopa lubrica</i>	—	—	—	2	—	1	—	—	—	—	0.3	20	0.4	
Number of snails, recalculated, Σ . .	96	27	36	53	11	65	32	26	57	212	61.5			
<i>Limax cinereo-niger</i> Wolf	1	—	—	—	—	1	1	—	1	—		50		
<i>Arion ater</i> (L.)	—	—	—	—	—	—	1	—	—	1		20		
<i>A. subfuscus</i>	—	—	—	—	1	—	—	—	—	—		10		
Number of species	5	4	6	5	5	9	8	5	6	7				

Tab. 3. Environmental conditions in the drier mixed wood series. The localities are arranged according to increasing Ca content in the foena. Explanation of symbols: 1 = sparse, 2 = relatively abundant, 3 = dominating (for wood litter: 3 = very abundant); moss layer: 1 = thin, 2 = relatively thick, 3 = thick; light conditions: 1-5 (1 = very shady, 5 = very exposed); soil moisture: 1-5 (1 = very dry, 5 = wet).

Habitat characteristics	Locality No.											Average
	53	50	57	55	21	43	52	36	46	48	56	
Coniferous trees												
<i>Picea abies</i>	3	3	3	3	3	3	3	3	2	3	3	
<i>Pinus silvestris</i>	2	2	2	1	2	1	-	-	2	1	-	
Deciduous trees, totally	1	1	2	2	2	2	2	2	2	2	2	
<i>Betula</i>	1	1	2	2	2	2	2	2	2	2	2	
<i>Quercus</i>	1	1	1	1	1	1	1	1	1	1	1	
<i>Salix</i> spp.	1	-	-	1	1	-	-	-	-	-	1	
<i>Populus tremula</i> L.	-	-	1	-	-	-	-	1	-	-	-	
Oligotrophic plants												
<i>Vaccinium myrtillus</i> and												
<i>V. vitis idaea</i>	2	2	2	3	2	4	2	3	3	3	3	
<i>Deschampsia flexuosa</i>	1	1	1	1	1	1	1	1	1	1	1	
Mesotrophic plants												
<i>Pteridium aquilinum</i> (L.)	-	-	2	1	2	-	-	2	-	-	1	
Others (<i>Luzula pilosa</i> (L.),												
<i>Oxalis</i> , etc.).....	-	-	1	-	2	-	-	2	1	-	1	
Moss layer.....	3	3	2	3	2	3	2	3	3	3	3	
Light conditions.....	2-3	4	4	4	2	3	3	3	4	4	4	
Amount of wood litter.....	1	2	2	2	3	1	2	1	1	1	2	
Soil moisture.....	3-4	4	3-4	3	3	3	2-3	3	3	3-4	4	
Thickness of organic layer, cm	20	10	3	9	5	15	12	4	15	12	15	
Leached zone, cm.....	20	15*	1	9	4	>20	4	3	3	3	>20	
Ca, %												
in the foena.....	5.6	5.7	5.8	6.3	6.6	7.1	7.6	8.1	8.3	8.6	9.9	7.2
in mineral soil (leached zone)	0.5	1.1	1.1	0.6	0.7	1.0	1.1	0.9	0.7	0.4	0.4	0.8
pH												
in surface of soil.....	4.0	4.5	5.0	4.5	5.0	4.5	4.3	4.3	4.5	4.3	4.8	4.5
in the leached zone.....	5.0	5.0	4.8	5.0	4.5	4.8	4.3	4.5	4.8	4.3	4.8	4.8
in the accumulation zone...	-	-	5.0	5.0	6.0	-	5.5	4.8	4.8	4.5	-	(5.1)

* above the leached soil horizon a mould-like earth (10 cm, pH about 4.8).

Tab. 4. The mollusc fauna of the drier mixed wood series. The individual numbers are recalculated to correspond to a sample volume of 3 l. Mi = mean number of individuals/locality. C = constancy. Dm = dominance value, average for the species. + = shells from dead snails only. I = few individuals, II = abundant. The localities are arranged according to increasing Ca content in the foena.

Species	Locality No.											Mi	C %	Dm
	53	50	57	55	21	43	52	36	46	48	56			
<i>Nesovitrea hammonis</i>	+	18	50	13	12	22	25	41	62	65	15	29.4	100	46.7
<i>Euconulus f. fulvus</i>	3	11	9	5	13	8	7	22	17	11	9	10.4	100	27.3
<i>Columella aspera</i>	+	25	12	2	7	5	5	14	13	14	5	9.3	100	15.0
<i>Vertigo substriata</i>	-	-	3	2	2	1	2	4	13	7	3	3.4	82	5.1
<i>Discus ruders</i>	-	1	1	-	11	-	-	7	-	1	-	1.9	45	3.1
<i>Vertigo ronneyensis</i>	-	11	-	-	-	-	-	1	6	-	-	1.6	27	2.1
<i>Oxychilus alliarius</i>	-	-	-	-	-	-	-	-	-	5	+	0.5	18	0.4
<i>Clausilia bidentata</i>	-	-	-	-	2	-	-	-	-	-	-	0.2	9	0.4
<i>Punctum pygmaeum</i>	-	-	-	-	-	-	-	1	-	-	-	0.1	9	0.1
Number of snails, recalculated, Σ	3	64	75	23	47	35	39	89	106	107	32	56.3		
<i>Limax cinereo-niger</i>	-	-	-	I	I	-	-	-	I	I	-		36	
<i>Arion subfuscus</i>	-	-	-	-	-	-	I	-	I	-	I		27	
<i>A. ater</i>	-	-	-	-	I	I	-	-	-	-	-		18	
<i>Limax marginatus</i> (Müll.)	-	-	-	-	-	-	-	I	-	-	I		18	
<i>L. tenellus</i>	-	-	-	-	-	-	I	-	-	-	-		9	
<i>Arion circumscriptus</i>	-	-	-	-	-	-	-	I	-	-	-		9	
<i>f. silvatica</i> Lohm.	-	-	-	-	-	-	-	I	-	-	-		9	
Number of species	3	5	5	5	8	5	6	8	6	8	8			

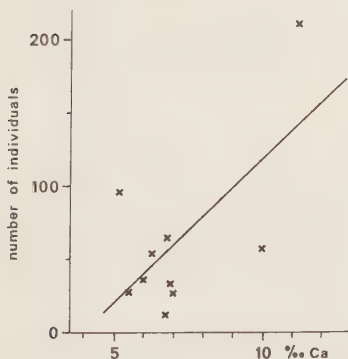


Fig. 7. Numbers of snails in relation to Ca content of the foena in the moist mixed wood series. The individual numbers have been recalculated to correspond to a sample volume of 3 l. The correlation coefficient is 0.646, $p < 0.05$. Regression line $y = 19.5x - 77.0$.

icant is the correlation between species number and Ca content in the foena.

Although locality 52 is somewhat drier, the mollusc fauna does not deviate. The soil moisture might not within the series have any greater importance as a limiting factor. The thick moss probably protects against drought.

From the dominant identity and resemblances in species composition and from the habitat data (Tab. 3) may be read, that localities with an oligotrophic vegetation poor in plant species may have a very poor mollusc fauna (locality 53, low in Ca) or a rich fauna (loc. 48, rich in Ca). Gradations between these extremes occur (loc. 55, 43, 52 and 46). A fauna surprisingly poor in individuals was found at the most Ca-rich locality (56: in a large grove surrounded with heath-like ground). Deviating mollusc faunas were found at locality 21, where there was plenty of dead wood from deciduous trees, and at loc. 50, where the mould-like earth over the leached zone was possibly favourable. In comparison with e.g. the meadow wood series the drier mixed wood series is rather homogeneous.

Characteristic species is *Vertigo ronney-*

Tab. 5. Environmental conditions in the oak wood series. The localities are arranged according to increasing Ca content in the foena. Explanation of symbols: 1 = sparse, 2 = relatively abundant, 3 = dominating (for rocks, leaf litter & foena and wood litter: 3 = very abundant); light conditions: 1-5 (1 = very shady, 5 = very exposed); soil moisture: 1-5 (1 = very dry, 5 = wet).

Habitat characteristics	Locality No.										20 Average
	74	79	66	78	77	65	51	54	71		
Direction of slope	(NW)	E	WSW	- (WSW)	WNW	- (SE)	- (SW)				
Occurrence of rocks	-	1	1	-	1	1	1	1	2	2	
<i>Quercus</i> spp.	3	3	3	3	3	3	3	3	3	3	
Other deciduous trees, totally	2	2	2	2	1	2	1	2	2	2	
<i>Populus tremula</i>	1	-	-	1	-	1	-	1	-	-	
<i>Corylus</i>	-	1	1	1	-	1	-	-	-	-	
Coniferous trees (<i>Picea</i>)	-	1	1	1	1	-	1	1	1	1	
Undergrowth, totally	2	2	1	2	3	2	2	1	1	2	
<i>Vaccinium myrtillus</i>	2	2	2	2	1	1	1	2	2	1	
<i>Deschampsia flexuosa</i>	1	2	-	1	1	2	2	1	2	-	
<i>Melampyrum pratense</i> L.	1	-	1	1	3	2	2	1	-	1	
<i>Convallaria majalis</i> L.	-	1	1	3	1	1	2	3	1	3	
Others (<i>Oxalis</i> , <i>Veronica chamaedrys</i> L., <i>Solidago</i> , etc.)	2	2	1	2	1	1	2	-	-	2	
Mosses	1	1	1	1	1	1	1	-	-	1	
Light conditions	3	2	4	4	3	4	3	3	2	2	
Litter & foena	1	2-3	1-2	1-2	2	1-2	1-2	1	3	1	
Amount of wood litter	3	1	1	1	1	2	2	2	1	1	
Soil moisture	3	3-4	2	2	2	3	2-3	3	3-4	3	
Thickness of the mould layer, cm.	15	4	40	8	12	15	7	15	12	7	
Ca, ‰											
in the foena	5.5	6.5	7.3	7.4	9.0	9.6	10.2	10.9	14.5	14.8	9.6
in the mould	1.0	0.9	1.9	1.4	1.1	1.2	0.6	0.9	1.0	0.8	1.2
pH											
in surface of soil	4.8	5.8	4.8	4.5	4.8	4.5	6.3	4.5	4.5	5.0	4.9
at a depth of about 10 cm.	4.8	4.8	4.5	4.5	4.5	4.5	5.3	4.8	4.8	4.8	4.7

ensis (Westerl.), not found in any other series. In conformity with the moist mixed wood series there are few species and individuals. *Discus ruderatus* (Hartm.) reaches slightly greater numbers than in the oak wood series.

5.3. The oak wood series

Ten localities were investigated (series C, Fig. 1). The ground was more or less hilly. Brown, often rather thin layers of mould were found at all localities. No podzolization was observed. Tab. 5 gives a survey of habitat data. The calcium content of the foena was high; the mean (9.6‰) is near those of the two meadow wood series.

The mollusc fauna is presented in Tab. 6. Dominant identity (Fig. 6) and species identity (Jaccard 1928) were calculated for all locality

combinations. The fauna of this series is remarkably uniform. All the species reach a greater average abundance in the meadow wood series. The fauna of the oak woods differs from those of the two first series mainly by *Punctum pygmaeum* (Drap.) and *Cochlicopa lubrica* (Müll.) being eu-constant (>75% constancy).

The correlation between Ca content and snail numbers is illustrated in Fig. 8. Localities 20 and 71 had approximately equal Ca content. The high number of individuals at the former may be ascribed to the higher pH and the admixture of aspen leaves in the oak foena.

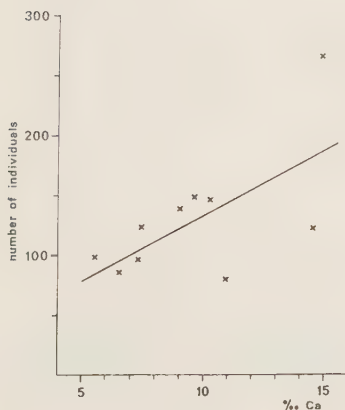
Two localities (71 and 79) had a somewhat greater soil moisture than the others. This had no distinct effect on their mollusc faunas.

Tab. 6. The mollusc fauna of the oak wood series. The individual numbers have been recalculated to correspond to a sample volume of 3 l. Mi = mean number of individuals/locality. C = constancy. Dm = dominance value, average for the species. + = shells from dead snails. I = few individuals. II = abundant. The localities are arranged according to increasing Ca content in the foerna.

Species	Locality No.										Mi	C %	Dm
	74	79	66	78	77	65	51	54	71	20			
<i>Nesovitrea hammonis</i>	52	46	43	75	74	61	55	47	41	122	61.6	100	48.7
<i>Euconulus f. fulvus</i>	7	21	30	32	26	39	22	9	20	63	26.9	100	20.3
<i>Columella aspera</i>	23	5	8	6	7	18	17	8	+	25	11.7	100	9.2
<i>Punctum pygmaeum</i>	6	8	2	2	16	11	23	4	29	24	12.5	100	9.1
<i>Cochlicopa lubrica</i>	1	3	3	5*	—	1	3	2	2	15	3.5	90	2.3
<i>Verigo substriata</i>	8	—	1	—	12	3	15	9	11	18	7.7	80	5.7
<i>Clausilia bidentata</i>	—	—	—	—	—	9	9	—	7	—	2.5	30	1.9
<i>Discus rudersatus</i>	—	—	1	—	—	2	—	6	—	—	0.9	30	0.7
<i>Vittrina pellucida</i>	—	—	1	2	—	—	—	—	+	—	0.3	30	0.2
<i>Discus rotundatus</i>	—	—	—	—	5	—	—	8	—	—	1.3	20	1.0
<i>Oxychilus alliarius</i>	—	—	+	1	—	—	—	—	—	—	0.1	20	0.1
<i>Cepaea hortensis</i>	—	—	—	—	+	+	—	—	—	—	0.0	20	0.0
<i>Vitrea contracta</i>	—	1**	—	—	—	—	—	—	—	—	0.1	10	0.1
<i>Bradybaena fruticum</i> (Müll.) ..	—	—	+	—	—	—	—	—	—	—	0.0	10	0.0
<i>Arianta arbustorum</i>	—	—	+	—	—	—	—	—	—	—	0.0	10	0.0
Number of snails, recalculated, Σ	97	84	95	122	139	148	146	79	122	266	129.8		
<i>Limax marginatus</i>	—	—	—	I	I	I	I	—	—	—		40	
<i>Arion circumscriptus f. silvatica</i>	I	—	—	—	I	I	—	—	—	—		30	
<i>A. ater</i>	—	—	—	—	I	I	—	—	—	—		20	
<i>Limax cinereo-niger</i>	I	—	—	I	—	—	—	—	—	—		20	
<i>Arion subfuscus</i>	—	1	—	—	—	—	—	—	—	—		10	
Number of species	8	7	9	9	10	12	10	6	9	7			

* *Cochlicopa* sp. (small specimens, probably near to *C. lubrica*; cf. Waldén 1966 a: 51).

** probably a straggler from an adjacent meadow wood locality.



5.4. The meadow wood series

The 24 localities have been grouped into a dry and a moist series. All localities are situated in deciduous meadow woods on the slopes of greenstone ridges. Thick layers of brown to black mould occurred. The most characteristic tree was lime. The ground flora was rich in herbs and grass. Habitat data for the dry series are given in Tab. 7 and for the moist one in Tab. 9. The sampling squares were very uniform, at least floristically. The soil moisture varied a good deal within the squares.

Fig. 8. The abundance of snails in relation to Ca content of the foerna in the oak wood series. The numbers have been recalculated to correspond to a sample volume of 3 l. The correlation coefficient is 0.638, $p < 0.05$. Regression line $y = 10.9x + 23.4$.

Tab. 7. Environmental conditions in the dry meadow wood series. The localities are arranged according to increasing soil moisture. Explanation of symbols: 1 = sparse, 2 = relatively abundant, 3 = dominating (for rocks, leaf litter & foena and wood litter: 3 = very abundant); light conditions: 1-5 (1 very shady, 5 = very exposed); foena: + = rich in decaying twigs; soil moisture: + = great variation, ++ = very great variation. The herbs listed constitute only a small selection. All of them also occur in the moist meadow wood series.

Habitat characteristics	Locality No.												Average
	39	68	33	12	37	34	49	9	30	35	47	32	
Direction of slope	SE	SE	SE	WNW	(S)	W	W	SSW	W	SE	NE	NW	SE
Occurrence of rocks	2	1	3	3	3	1	2	1	2	2	3	3	
Deciduous trees													
<i>Tilia</i>	2	3	2	2	2	3	3	2	3	3	3	3	3
<i>Fraxinus</i>	-	1	-	2	-	1	-	-	1	1	1	1	2
<i>Acer</i>	1	-	1	-	1	-	2	1	1	-	2	1	
<i>Carpinus</i>	3	-	3	-	-	2	1	-	-	-	-	-	-
<i>Quercus</i> (and <i>Fagus</i>)	-	2	2	2	3	2	2	2	2	2	2	2	2
<i>Corylus</i>	1	1	1	1	2	2	-	-	2	2	2	2	1
<i>Betula</i>	1	-	-	-	1	1	-	-	1	1	-	-	-
Coniferous trees (<i>Picea</i>)	1	-	1	1	1	1	1	-	1	1	1	1	1
Herbs, totally	3	2	2	1	1	3	3	2	2	2	3	2	
a) eutrophic plants													
<i>Mercurialis perennis</i> L.	-	-	-	-	-	-	-	2	-	-	-	3	
<i>Campanula trachelium</i> L.	1	-	-	-	-	-	1	-	-	-	3	-	
<i>Anemone hepatica</i> L.	-	-	1	-	2	2	1	-	2	-	1	2	
<i>Poa nemoralis</i> L.	1	1	1	1	1	1	2	-	1	-	1	1	
<i>Lathyrus vernus</i> (L.)	3	-	1	-	-	2	1	-	-	-	-	-	
<i>Paris quadrifolia</i> L.	1	-	-	-	-	-	-	-	3	-	-	-	
<i>Aegopodium podagraria</i> L.	-	-	-	-	3	-	-	1	1	1	2	1	
b) mesotrophic plants													
<i>Oxalis acetosella</i> L.	1	-	3	-	2	-	1	1	-	2	1	-	
<i>Melampyrum sylvaticum</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Convallaria</i> , etc.	1	1	-	2	1	1	1	1	1	-	-	-	
Mosses	2	-	-	-	-	-	-	-	-	1	2	-	
Light conditions	3	4-5	1	3	4	2	4	2	4	3-5	1	3	4
Litter & foena	1	1	3	2	3	2	1-3	1	1	1	1-2	1-2	1
Amount of wood litter	1	2	1	1	1	1	2	2	2	2	2	1	1
Ca, %													
in the foena	7.0	12.0	7.1	10.3	13.0	6.4	6.6	8.6	11.0	6.9	13.0	11.4	9.4
in the mould	5.0	4.8	4.5	2.0	3.1	4.1	3.5	3.0	8.0	2.0	3.9	6.0	4.2
pH													
in surface of soil	5.5	6.5	6.5	5.5	5.5	6.5	6.5	6.0	6.5	5.7	6.8	6.2	6.1
at a depth of about 10 cm	5.5	5.0	4.5	4.5	4.8	4.8	5.3	5.0	5.0	4.5	5.0	4.5	4.9
Soil moisture, %													
average (18.8.1966)	25	27	27	29	30	31	32	32	32	33	34	35	

5.5. The dry meadow wood series

Twelve localities with mean values of soil moisture <35% were included (series D, Fig. 1). The mollusc fauna (Tab. 8) consisted of 28 species of snails and nine species of slugs. Sixteen of the species were found only in the meadow wood series. All the snail species occurred also in the moist series.

The abundance of snails was not correlated

to the Ca content of the foena. The moisture was more important (Fig. 9).

5.6. The moist meadow wood series

Twelve localities (soil moisture >35%) were included (series E, Fig. 1). This series had most species: 31 snails and nine slugs (Tab. 10). It also had most individuals; the mean was 634 per sample while in the dry series it was 367.

Tab. 8. The mollusc fauna of the dry meadow wood series. The individual numbers are recalculated to correspond to a sample volume of 3 l. Mi = mean number of individuals/locality. C = constancy. Dm = dominance value, average for the species. + = shells from dead snails or found on a second visit to the locality. I = few individuals, II = abundant and III = very abundant. The localities are arranged according to increasing soil moisture.

Species	Locality No.													Mi	C %	Dm
	39	68	33	12	37	34	49	9	30	35	47	32				
<i>Nesovitrea hammonis</i>	64	38	45	70	45	52	57	85	125	14	52	182	69.1	100	20.5	
<i>Punctum pygmaeum</i>	22	13	15	51	37	138	48	115	67	21	120	77	60.3	100	16.7	
<i>Euconulus f. fulvus</i>	9	20	15	45	49	41	21	57	104	6	37	126	44.1	100	11.5	
<i>Cochlicopa lubrica</i>	3	1	5	14	2	20	3	18	29	7	22	36	13.3	100	4.4	
<i>Columella aspera</i>	9	2	2	5	15	24	8	3	46	3	4	33	12.8	100	3.1	
<i>Clausilia bidentata</i>	4	8	3	9	6	12	10	5	16	13	13	28	10.6	100	3.0	
<i>Vertigo substriata</i>	6	2	2	15	8	4	7	12	9	3	11	19	8.2	100	2.3	
<i>Discus rotundatus</i>	9	4	13	1	58	—	3	58	41	2	5	34	19.0	92	4.9	
<i>Cepaea hortensis</i>	—	+	3	1	—	+	+	+	3	2	2	6	1.4	92	0.4	
<i>Discus rudatus</i>	14	8	—	3	+	7	—	12	2	23	3	2	6.0	83	1.9	
<i>Nesovitrea petronella</i>	25	—	—	—	—	27	21	+	22	39	13	21	14.0	67	3.8	
<i>Vitrina pellucida</i>	—	2	+	2	—	—	3	+	2	4	—	2	1.2	67	0.3	
<i>Aegopinella pura</i>	2	20	6	—	42	—	35	—	15	—	—	15	12.1	58	3.8	
<i>Cochlicopa lubricella</i>	1	2	—	—	—	—	4	13	—	—	41	1	5.2	58	1.4	
<i>Vertigo pusilla</i>	—	2	+	8	—	1	—	—	4	—	4	2	1.8	58	0.5	
<i>Carychium tridentatum</i>	—	45	—	—	88	—	3	93	—	201	—	227	54.8	50	11.8	
<i>Vitrea crystallina</i>	10	—	—	22	37	56	5	—	—	117	—	—	20.6	50	5.5	
<i>Arianta arbustorum</i>	3	—	+	+	—	—	2	—	—	—	—	—	0.4	50	0.2	
<i>Cochlodina laminata</i>	12	—	3	2	6	—	15	—	—	—	—	—	3.2	42	1.3	
<i>Vitrea contracta</i>	—	—	4	—	—	—	—	6	3	—	8	1	1.8	42	0.6	
<i>Helicigona lapicida</i> (L.)	3	2	—	—	—	—	—	—	2	—	2	1	0.8	42	0.3	
<i>Acanthinula aculeata</i>	6	—	10	—	1	—	33	—	—	—	—	—	4.2	33	1.8	
<i>Iphigenia plicatula</i>	6	—	2	—	—	—	9	—	—	—	—	—	1.4	33	0.7	
<i>Oxychilus alliarius</i>	—	—	—	—	2	—	—	7	—	+	—	—	0.8	25	0.2	
<i>Bradybaena fruticum</i>	—	2	—	—	—	—	—	—	—	—	+	1	0.3	25	0.1	
<i>Vallonia excentrica</i>	—	—	—	—	—	+	—	—	—	—	+	—	0.0	17	0.0	
<i>Aegopinella nitidula</i>	—	—	1	—	—	—	—	—	—	—	—	—	0.1	8	0.1	
<i>Trichia hispida</i>	—	—	—	—	—	—	—	+	—	—	—	—	0.0	8	0.0	
Number of snails, recalculated, Σ	207	169	126	247	397	385	281	476	501	454	336	817	367			
<i>Arion circumscriptus</i>																
<i>f. silvatica</i>	I	—	—	—	I	I	I	—	—	I	I	—	50			
<i>A. ater</i>	I	—	—	I	—	—	—	I	I	—	—	I	42			
<i>A. subfuscus</i>	—	I	—	—	I	—	I	—	—	—	I	—	33			
<i>A. c. circumscriptus</i> (Johnst.)	—	I	—	—	—	—	—	I	I	—	—	I	33			
<i>Limax cinereo-niger</i>	—	—	—	I	—	—	—	—	—	—	I	I	25			
<i>L. marginatus</i>	—	—	—	—	—	—	—	—	I	I	I	—	25			
<i>Arion fasciatus</i>	—	—	—	—	—	I	—	I	—	II	—	—	17			
<i>Limax tenellus</i>	—	I	—	—	—	I	—	—	—	—	—	—	8			
<i>Deroceras agreste</i> (L.)	—	—	—	—	—	—	—	—	—	I	—	—				
Number of species	21	20	18	16	19	17	20	20	20	19	22	22				

Ca may in this series have importance as a limiting factor. The correlation between Ca content and abundance is, however, not statistically significant. At the two localities, which had the greatest number of individuals, the very small species *Carychium tridentatum*

(Risso) and *Punctum pygmaeum* constituted more than half the number.

No correlation was found between abundance and soil moisture in the series. Still it is probable that it is of importance for many of the species. The light conditions may also

Tab. 9. Environmental conditions in the moist meadow wood series. The localities are arranged according to increasing soil moisture. Explanation of symbols: 1 = sparse, 2 = relatively abundant, 3 = dominating (for rocks, leaf litter & foena and wood litter: 3 = very abundant); light conditions: 1-5 (1 = very shady, 5 = very exposed); foena: * = mainly decaying twigs; soil moisture: + = great variation, ++ = very great variation. - The herbs listed constitute only a small selection. Most of them also occur in the dry meadow wood series.

Habitat characteristics	Locality No.												
	10	16	44	67	42	38	45	31	70	41	40	13	Average
Direction of slope	SE	E	E	NE	WNW	SE	E	SE	SW	WNW	NW	E	
Occurrence of rocks	3	3	2	2	3	2	2	2	3	2	2	3	
Deciduous trees													
<i>Tilia</i>	2	3	3		2	3	-	3	3	2	2		
<i>Fraxinus</i>		2	-	2		1	-	-	-	-	-	-	
<i>Acer</i>	1	-	1	-	2	1	3	1	1	1	2	1	
<i>Ulmus</i>	-	-	-	-	2	1	1	1	1	3	1	-	
<i>Carpinus</i>	3	-	1	-	-	-	-	-	-	-	-	-	
<i>Quercus</i> (and <i>Fagus</i>)	2	2	2	3	3	2	1	2	2	2	3	1	
<i>Corylus</i>	1	1	1	2	1	-	2	-	2	1	1	-	
<i>Betula</i>	1	1	-	1	1	1	-	1	-	-	-	1	
Coniferous trees (<i>Picea</i>)	1	-	1	1	1	1	1	1	1	-	1	2	
Herbs, totally	2	2	3	3	2	2	2	2	1	3	3	2	
a) eutrophic plants													
<i>Mercurialis perennis</i>	-	-	-	-	-	-	-	3	-	-	-	-	
<i>Campanula trachelium</i>	1	-	-	1	1	1	-	2	1	1	-	-	
<i>Anemone hepatica</i>	2	-	-	-	-	-	-	-	3	-	-	-	
<i>Cardamine bulbifera</i> (L.)	-	-	-	-	-	-	-	-	-	1	3	-	
<i>Pulmonaria officinalis</i> L.	-	-	-	-	-	-	-	-	-	3	-	-	
<i>Campanula latifolia</i> L.	-	-	2	-	-	-	-	-	-	1	-	-	
<i>Aegopodium podagraria</i>	-	-	-	1	-	2	1	-	-	1	-	-	
b) mesotrophic plants													
<i>Oxalis acetosella</i>	2	2	3	3	-	-	3	-	-	-	-	3	
<i>Melampyrum silvaticum</i>	1	1	-	-	2	1	-	2	-	-	-	-	
<i>Convallaria</i> , etc.	-	-	-	2	-	-	-	-	-	-	-	-	
Mosses	1	2-3	3	2	2	1	2	4	3	3	4	3	
Light conditions	3	1-3	1-2	1	1-2	1-3	2	3	1	1	1	2	
Litter & foena	1	1	2	2	2	1	2	1	2	2	2	2	
Amount of wood litter	7.3	11.7	9.4	6.4	9.3	9.2	9.1	8.9	8.6	15.6	12.0	12.6	10.0
Ca, %	2.7	2.4	5.5	2.4	6.7	5.0	2.4	9.5	2.4	6.3	3.0	2.3	4.1
pH													
in surface of soil	5.5	6.3	5.8	6.5	6.3	6.5	5.0	5.8	4.8	8.0	5.7	7.0	6.1
at a depth of about 10 cm	4.5	4.8	4.5	5.0	5.0	5.0	4.8	4.3	4.5	5.5	4.8	5.8	4.9
Soil moisture, %													
average (18.8.1966)	35	36++	36+	36	38	40+	41	46++	46++	48+	53	54++	

influence the abundance, probably because most shady localities have a high RH.

5.7. The distribution of molluscs within the meadow wood series

The 24 meadow wood localities were also grouped into one series that is poor and another that is relatively rich in calcium in the foena layer (Tab. 11). Twenty-one of the snail species had a higher and ten a lower

average individual number per sample in the Ca-rich series.

Dominant identity and also species identity according to Jaccard (1928) have been calculated for all the 24 localities (Fig. 10). The species identity between two localities is the percentage of species occurring at both computed on the total number of species at the two localities.

In Fig. 10 three locality groups may be

Tab. 10. The mollusc fauna of the moist meadow wood series. The individual numbers have been recalculated to correspond to a sample volume of 3 l. Mi = mean number of individuals/locality. C = constancy. Dm = dominance value, average for the species. + = shells from dead snails or found on a second visit to the locality. I = few individuals, II = abundant and III = very abundant. The localities are arranged according to increasing soil moisture.

Species	Locality No.													Mi	C %	Dm
	10	16	44	67	42	38	45	31	70	41	40	13				
<i>Punctum pygmaeum</i>	45	561	79	12	209	87	94	115	9	67	28	217	127.0	100	20.0	
<i>Nesovitrea hammonis</i>	14	29	111	36	57	18	31	196	26	27	33	48	52.2	100	11.9	
<i>Euconulus f. fulvus</i>	16	183	35	5	44	45	31	69	7	1	28	66	44.2	100	7.2	
<i>Cochlicopa lubrica</i>	3	30	35	11	11	84	40	11	8	23	110	18	32.0	100	5.4	
<i>Vertigo substriata</i>	5	41	34	12	35	6	24	36	1	2	12	89	24.7	100	4.5	
<i>Nesovitrea petronella</i>	1	44	21	6	9	53	41	—	5	71	54	17	26.8	92	4.3	
<i>Columella aspera</i>	8	1	22	1	45	+	15	45	2	—	3	33	14.6	92	3.2	
<i>Clausilia bidentata</i>	2	10	15	—	5	15	2	18	2	12	16	24	10.1	92	1.6	
<i>Carychium tridentatum</i>	45	230	—	96	14	1290	—	42	33	354	258	5	197.4	83	22.5	
<i>Discus rotundatus</i>	15	57	—	1	4	—	6	2	11	2	—	—	12	9.2	83	1.6
<i>Vertigo pusilla</i>	2	5	2	1	2	—	—	14	—	1	3	4	2.8	75	0.5	
<i>Discus ruderatus</i>	—	16	—	—	—	7	5	—	2	+	5	17	4.3	67	0.7	
<i>Vitrina pellucida</i>	—	9	6	1	—	+	+	—	—	—	5	4	2.7	67	0.4	
<i>Cochlicopa lubricella</i>	—	3	142	—	14	7	36	—	—	238	63	—	41.9	53	6.4	
<i>Vitrea contracta</i>	—	9	+	—	11	17	21	—	—	13	10	—	6.7	58	1.1	
<i>Cepaea hortensis</i>	—	—	+	—	—	2	+	9	—	—	4	1	1.3	58	0.2	
<i>Helicigona lapicida</i>	+	+	—	—	6	+	—	—	—	—	—	5	0.9	42	0.2	
<i>Vitrea crystallina</i>	14	—	—	58	—	45	—	—	—	—	—	9	10.5	33	2.5	
<i>Aegopinella pura</i>	3	—	—	34	—	—	—	1	—	—	—	65	8.6	33	1.9	
<i>Bradybaena fruticum</i>	—	—	—	—	—	1	—	3	—	8	8	—	1.7	33	0.2	
<i>Oxychilus alliarius</i>	1	—	—	—	—	—	2	1	—	—	—	4	0.7	33	0.1	
<i>Cochlodina laminata</i>	3	—	—	4	—	—	—	—	—	—	—	17	2.0	25	0.5	
<i>Arianta arbustorum</i>	2	—	—	2	—	+	—	—	—	—	—	—	0.3	25	0.1	
<i>Trichia hispida</i>	—	—	—	—	—	—	—	—	—	93	33	—	10.5	17	1.3	
<i>Columella edentula</i>	4	—	—	22	—	—	—	—	—	—	—	—	2.2	17	0.8	
<i>Iphigenia plicatula</i>	+	—	—	4	—	—	—	—	—	—	—	—	0.3	17	0.1	
<i>Vertigo alpestris</i> Alder	—	—	—	—	—	—	—	—	—	2	2	—	0.3	17	0.04	
<i>Vallonia excentrica</i>	—	—	1	—	—	+	—	—	—	—	—	—	0.1	17	0.02	
<i>Aegopinella nitidula</i>	16	—	—	—	—	—	—	—	—	—	—	—	1.3	8	0.7	
<i>Acanthinula aculeata</i>	6	—	—	—	—	—	—	—	—	—	—	—	0.5	8	0.2	
<i>Vertigo pygmaea</i>	—	—	—	—	—	—	—	—	—	1	—	—	0.1	8	0.01	
Number of snails, recalculated, Σ	205	1191	505	308	463	1685	352	568	95	910	673	656	634			
<i>Arion circumscriptus</i>																
<i>f. silvatica</i>	II	—	I	—	I	I	I	I	—	—	I	—	—	58		
<i>A. subfuscus</i>	—	—	I	—	—	I	I	I	—	—	I	—	—	33		
<i>Limax marginatus</i>	—	—	—	—	—	I	—	I	—	I	I	II	—	33		
<i>Arion ater</i>	I	—	—	—	I	—	I	—	—	—	I	—	—	33		
<i>A. fasciatus</i>	—	—	—	—	—	I	—	—	II	III	II	—	—	33		
<i>Limax tenellus</i>	—	—	—	—	—	I	I	—	I	—	—	—	—	25		
<i>Arion c. circumscriptus</i>	—	—	—	—	—	—	—	I	—	I	—	—	—	17		
<i>Limax cinereo-niger</i>	I	—	—	—	—	—	—	—	—	—	—	—	—	8		
<i>Decoceras laeve</i> (Müll.)	—	—	—	—	—	—	—	—	—	I	—	—	—	8		
Number of species	24	16	16	18	17	25	19	16	15	20	23	20				

discussed. The localities in group I are all situated in the northern part of the greenstone course. They had a relatively low Ca content and soil moisture and most of them were shady. The snail fauna is characterized

by the species *Cochlodina laminata* (Mont.), *Vitrea crystallina* (Müll.), *Aegopinella pura* (Alder) and *Arianta arbustorum* (L.). *Acanthinula aculeata* (Müll.), *Iphigenia plicatula* (Drap.), *Aegopinella nitidula* (Drap.) and Co-

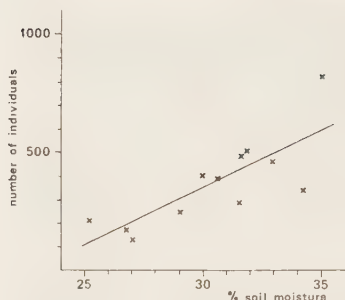


Fig. 9. Abundance of snails in relation to soil moisture in the dry meadow wood series. The individual numbers have been recalculated to correspond to a sample volume of 3 l. The soil moisture values refer to the upper layer of mould (3 cm). The correlation coefficient is 0.789, $p < 0.01$. Regression line $y = 48.8x - 1117$.

lumella edentula (Drap.) occurred only in this locality group.

Group II includes localities that in one way or another were somewhat less favourable. On an average they were rather exposed to light. The mollusc fauna is characterized by less demanding species here reaching high abundance, e.g. *Nesovitrea hammonis* (Ström), *Clausilia bidentata* (Ström), *Euconulus f. fulvus* (Müll.), *Columella aspera* Waldén, *Vertigo substriata* (Jeffr.) and *Punctum pygmaeum*. *Cochlicopa lubrica*, *Discus rotundatus* (Müll.), *D. rudersatus*, *Cepaea hortensis* (Müll.), *Vertigo pusilla* Müll., *Nesovitrea petronella* (Pfeiffer), *Carychium tridentatum* and *Vitrea pellucida* were also common.

The mollusc fauna within locality group III is characterized by *Cochlicopa lubricella* (Porro) and *Vitrea contracta* Westerl. *Nesovitrea petronella*, *Cochlicopa lubrica*, *Punctum pygmaeum* and *Euconulus f. fulvus* had a high abundance within the group. Most of these localities are situated in the southern part of the greenstone course, but No. 42 and 47, which both are quite typical, lie far to the north. The Ca content was on an average relatively high, the soil moisture was good and the localities were moderately shady.

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Tab. 11. The occurrence of the snail species of the meadow wood localities in relation to calcium-poor and calcium-rich habitats. Explanation of symbols: Mi = mean number of individuals/locality. C = constancy. The calcium-poor series includes localities with 6.4–9.2% Ca in the foena, viz. loc. Nos. 34, 67, 49, 35, 39, 33, 10, 9, 70, 31, 45 and 38 (arranged according to increasing Ca content). In the calcium-rich series there are localities with 9.3–15.6% Ca, viz. Nos. 42, 44, 12, 30, 32, 16, 68, 40, 13, 37, 47 and 41. – For locality descriptions, see Tabs. 7 and 9. The mollusc faunas are presented in Tabs. 8 and 10.

Species	Calcium-poor series		Calcium-rich series	
	Mi	C %	Mi	C %
<i>P. pygmaeum</i>	60.1	100	127.3	100
<i>N. hammonis</i>	53.3	100	68.1	100
<i>E. f. fulvus</i>	26.8	100	61.4	100
<i>C. lubrica</i>	17.0	100	27.6	100
<i>V. substriata</i>	9.8	100	23.1	100
<i>N. petronella</i>	18.2	83	22.7	75
<i>C. aspera</i>	9.3	100	17.4	92
<i>C. bidentata</i>	7.2	92	13.5	100
<i>C. tridentatum</i>	150.1	67	101.7	67
<i>D. rotundatus</i>	10.2	92	18.1	83
<i>V. pusilla</i>	1.5	42	2.8	83
<i>D. rudersatus</i>	5.8	67	4.7	83
<i>V. pellucida</i>	0.7	58	3.9	75
<i>C. lubricella</i>	4.0	42	43.1	75
<i>V. contracta</i>	4.0	33	4.6	67
<i>C. hortensis</i>	1.2	75	1.6	83
<i>H. lapicida</i>	0.3	25	1.5	58
<i>V. crystallina</i>	25.4	58	5.7	25
<i>A. pura</i>	6.7	50	13.1	42
<i>B. fruticum</i>	0.3	17	1.6	42
<i>O. allarius</i>	0.9	42	0.5	17
<i>C. laminata</i>	3.6	42	2.1	25
<i>A. arbustorum</i>	0.8	50	0.0	25
<i>T. hispida</i>	0.0	8	10.5	17
<i>C. edentula</i>	2.2	17	–	–
<i>I. plicatula</i>	1.8	42	–	–
<i>V. alpestris</i>	–	–	0.3	17
<i>V. excentrica</i>	0.0	17	0.1	17
<i>A. nitidula</i>	1.4	17	–	–
<i>A. aculeata</i>	4.6	33	0.1	8
<i>V. pygmaea</i>	–	–	0.1	8
Number of snails.....	440		576	
Number of species (slugs included), Σ.....	38		37	
Averages				
Ca, % in foena.....	7.7		11.8	
pH (in surface).....	5.8		6.3	
Soil moisture, %.....	35.3		37.4	

The localities 35 and 38, where *Carychium tridentatum* was co-dominant with *Vitrea*

Dominant identity								II								III								Loc. No.	
Locality group No. I																									
Loc. No.	33	39	49	37	67	10	13	12	31	70	30	32	68	9	34	16	47	42	45	44	41	40	38		35
35	15	33	25	44	37	37	23	26	23	55	20	46	46	35	38	37	20	18	23	20	58	62	61		35
38	16	18	17	36	46	37	18	18	20	52	20	46	38	35	21	19	20	19	20	19	54	58		67	38
40	19	28	28	40	49	41	26	25	28	64	33	55	48	43	31	42	40	28	47	40	75		75	57	40
41	16	23	22	35	42	36	19	15	22	53	22	46	42	36	22	38	32	23	33	45		82	70	50	41
44	51	53	57	38	28	39	51	63	51	64	65	56	44	49	54	37	68	55	64	65	81	60	56	44	
45	41	47	48	35	25	46	62	53	51	44	53	42	31	54	64	51	74	66		81	72	78	67	45	
42	43	41	47	41	29	50	70	55	63	41	56	50	39	58	70	69	74		72	71	67	72	70	58	42
47	52	46	53	38	25	46	67	63	59	49	62	54	46	63	76	63	74	70	68	56	64	81	52	47	
16	36	32	38	54	36	62	60	48	51	50	16	60	48	71	59		70	82	78	71	82	78	74	63	16
34	46	52	55	48	39	52	68	67	55	48	58	50	40	57		58	67	61	77	65	75	60	62	65	34
9	60	46	49	68	44	69	57	60	66	64	60	70	71	65	61	74	65	68	83	63	67	75	68	78	9
68	54	48	56	70	58	52	48	51	60	72	56	80		65	58	74	70	65	65	55	59	67	68	60	68
32	60	58	53	69	54	63	47	61	66	81	72		89	75	60	84	80	79	75	65	68	76	77	62	32
30	71	60	58	52	29	46	53	71	68	60		89	79	74	67	83	79	78	83	72	59	67	68	60	30
70	55	55	50	57	55	53	39	57	60		56	58	56	65	66	59	53	63	59	50	63	59	58	73	70
31	68	59	56	50	32	54	57	77	56	55	65	72	55	47		50	52	61	58	50	53	58	50	61	31
12	63	64	58	49	36	51	57		47	56	65	50	55	50	59	58	55	45	58	47	45	54	61	12	
13	47	42	61	50	36	54		65	65	58	71	73	71	64	57	67	54	62	67	52	54	59	65	79	13
10	46	46	49	71	52		80	52	60	59	46	42	42	41	40	57	44	60	50	43	45	44	54	50	10
67	30	33	41	64		78	75	68	50	59	52	58	52	46	45	60	44	48	52	45	55	52	59	57	67
37	54	45	51		59	65	71	63	65	64	48	50	54	57	50	48	48	45	50	35	35	40	54	68	37
49	64	67		75	71	69	68	57	52	53	52	54	52	54	48	48	46	50	48	45	38	44	58	65	49
39	65		76	71	61	67	65	57	44	50	64	58	56	52	60	52	64	54	42	34	37	42	63	54	39
33		65	75	65	66	63	54	63	52	38	62	56	55	50	43	48	57	50	54	52	38	44	46	45	33
	33	39	49	37	67	10	13	12	31	70	30	32	68	9	34	16	47	42	45	44	41	40	38	35	Loc. No.
	Species identity																								

crystallina, were very shady and had rich herb
floras.

From the above one can see that the mollusc fauna of the meadow wood series was rather heterogeneous. It might then be expected that the fauna was heterogeneously distributed also within the rather large sample squares. To cast light upon details in the distribution of the molluscs, small squares (50 × 50 cm) were laid out one or two years later in different microhabitats within the larger squares. At six of the localities 3–8 small squares were investigated. The fauna of the studied localities proved to be very homogeneous. In no case a species was abundant in some small squares and absent in others within the same locality. *Vitrea crystallina* had in the meadow wood series ten localities and *V. contracta* had twelve. Only one of these had both species:

they were, however, found there in all the three small squares.

Some mollusc species are most probably synanthropic within the area, as *Trichia hispida* (L.) and *Arion fasciatus* (Nilsson) (Lohmander 1953). *Vertigo pygmaea* (Drap.) and *Valonia excentrica* Sterki occur in meadows (former small tilled fields) near some of the meadow wood localities, and this element in the meadow wood series ought to depend upon invasion from such habitats.

6. Conclusions

Because the foena is much richer in calcium than the underlying mineral soil and the molluscs mainly feed on dead or withering plant material, attempts at estimating the importance of Ca for the molluscs fauna in CaCO_3 -

free habitats should be based on analyses of the Ca content in the foerna. Earlier the mollusc fauna has been related to the Ca content in mineral soil (Burch 1955).

In the oak wood series there is a high Ca oxalate content in the foerna. The much richer mollusc fauna in the meadow wood series may partly depend upon that Ca here mainly occurs as more soluble Ca salts, e.g. Ca citrate, which are more alkaline.

Shaded localities have often a high RH, even if their soil moisture is rather low. Some species generally considered as hygrophilous, e.g. *Vitrea crystallina*, had their greatest abundance in the dry meadow wood series, possibly because of a high RH at many of its localities.

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ON THE LIFE HISTORY OF COCHLICOPA LUBRICA (MÜLL.):

A BIOMETRICAL STUDY

Paper B

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ABSTRACT

Year classes of juveniles of Cochlicopa lubrica (Müll.) were discerned by measuring height and breadth and by counting whorls and winter lines in the shells. The annual number of juveniles per adult snail was small (1 - 14). The reproductive season comprises the summer and the autumn in southern Sweden, where juveniles need about 2.4 - 3.5 yr to reach adult stage. The growth rate appears to vary considerably between different geographical areas (England, Poland and Sweden).

INTRODUCTION

Cochlicopa lubrica (Müll.) is common in herb-rich deciduous woods in southern Sweden. In oligotrophic oak woods it has a rather high constancy but a low abundance. It is very sparse in oligotrophic coniferous forests (Wäreborn 1969). In open areas, e.g. meadows, it may be fairly abundant.

The species has been studied by Krull and Mapes (1952) and Kingston (1966) in the U.S.A., by Baker (1969, 1973) in England and by Umfiński and Focht (1979) in Poland. In England oviposition occurs all the year round, but two annual peaks in the reproduction were discerned. These peaks showed some variation in time (spring/late summer at a Norfolk locality and mid-winter/summer at a locality in Devon). Only one egg seemed to be laid at any one instant. Early hatched juveniles may in England become adult in the autumn of the same year. The growth period comprised almost the whole year at the two localities studied. In northern Poland C. lubrica was reported to need nearly two years to reach maturity, as indicated by the formation of the shell lip. Natality and mortality were estimated to be low. Kingston (1966) found that the species laid its eggs singly or in groups of 2 - 4, when reared in the laboratory.

The present study was performed in order to assess the reproduction period and the number of juveniles per adult C. lubrica in southern Sweden.

MATERIAL

Eight sift collections of C. lubrica from southern Sweden were obtained from the Natural History Museum of Gothenburg. They contained totally 177 adults and 851 juveniles and were collected at the end of each month, from May through October. Three samples

from October and one from each of the other months were studied. The samples were collected in different forest habitats, as classified in Tab. 1.

TABLE 1

Data on reproduction, age distribution and growth for Cochlicopa lubrica in southern Sweden in relation to time and type of locality. Type no. 1 = mesotrophic, 2 = eutrophic. The distribution of juveniles into year classes is based on winter lines, shell size and number of whorls.

Collection date	Type of locality		Number of adults	Number of juv. year No.				Number of juv. per 10 adults		First year juv.: Maximum shell height		Maximum growth (whorls)
	No.	pH		I	II	III	IV	2nd year	first year	mm		
21.05.1967	2	6.5	38	1	58	12	11	15.3		0.84		0.1
26.06.1971	1	6.5	9	4	41	12	1	45.6		0.87		0.2
28.07.1971	2	6.0	13	11	18	-	1	13.8		1.19		0.6
19.08.1965	2	7.0	14	31	1	1	3		22.1	1.37		0.8
29.09.1963	1	5.7	14	16	36	12	5	25.7		2.02		1.6
25.10.1973	2	7.5	21	283	18	17	2		135.0	2.42		1.9
31.10.1973	1	6.0	23	33	8	9	4		14.4	1.72		1.2
31.10.1970	2	7.7	45	200	3	5	-		44.4	2.39		2.0

METHODS

Height and breadth of the shells were measured. Whorls were counted according to Ehrmann (1956:21). More or less distinct "winter lines" were distinguished in the shells (Fig. 1). These lines are easy to see in young specimens of Cochlicopa lubrica and may still be discernible in most adult shells (cf. Pollard et al. 1977, Williamson 1979). Oosterhoff (1977) stated that in Cepaea nemoralis (L.) sometimes no line is formed during its first hibernation. In the very smooth shell of C. lubrica this line always appears to be clearly formed, while the second (or/ and the third) winter line rather often may be indistinct or missing. Shell size, number of whorls and existing lines have been used together to place the juvenile snails into their year

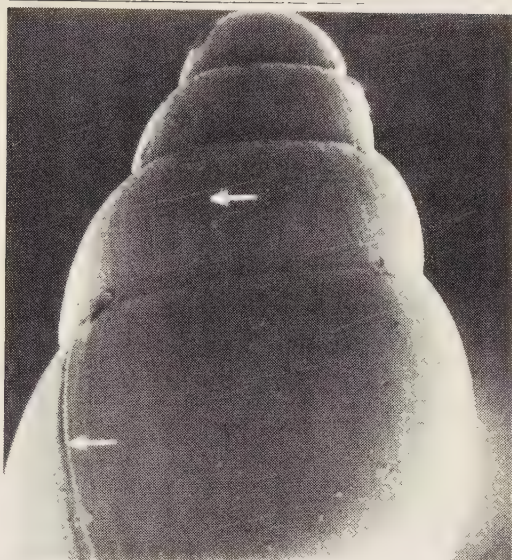


Fig.1. A third year juvenile of *Cochlicopa lubrica* (left x 17). In the greater magnification (right x 25) the winter lines are indicated by arrows. The proto-conch terminal line is to the right at the second whorl from the apex.

Photo: Dept. of Zoology, Lund.

classes. Wearing of the shell sometimes produces extra lines in adults; when the shell is corroded, all or most lines disappear. Such worn and corroded shells were omitted from the analysis of lines. A type of easily recognized lines were caused by transient shell peristome damages, apparently having negligible effects on the snail growth. These lines were excluded, while normal ones in the same shells were registered.

RESULTS

The distribution of lines in the shells is shown in Fig. 2. The juveniles reach adult stage after (or just before) their third winter season. It is possible to estimate the length of the juvenile period from available data. Individuals with the longest juvenile period may have hatched in early summer and become adult late in their fourth year, i.e. they have been juveniles for about 3.5 yr. Those which became adult late during their third year probably also have hatched from the eggs rather early, implying that they have spent about 2.4 yr as juveniles.

Data on reproduction, age distribution and growth are presented in Tab. 1. In the May and June samples there are very few first year juveniles; somewhat greater numbers appear in July. Two to six per cent of the first year juveniles in the three October samples are very small (≤ 0.2 whorls of growth). Reproduction may continue at a low level into November, provided that there is no frost. The number of juveniles per ten adults was found to be 14.4 - 135, i.e. 1 - 14 per adult snail per year. The growth of the first year juveniles is shown as observed maximum height of the shell and maximum number of growth whorls at the end of each month. Only seven first year juveniles out of 516 in the three October samples had > 1.8 growth whorls. It can be inferred from Fig. 2 that growth in the second and third year is about one whorl per year.

DISCUSSION

The observation that the first winter line practically always is very distinct agrees with the consistent trend in maximum shell height and maximum number of growth whorls of the first year juveniles in relation to time of the year (Tab. 1). Winter lines may, together with shell size and number of whorls, be used in growth studies and age determination of C. lubrica.

In comparison with larger snail species (e.g. Cepaea, Arianta) C. lubrica is not a prolific egg layer (Krull and Mapes 1952). Small species of terrestrial snails as a rule seem to have low numbers of eggs, cf. especially Frömming (1954) and also Steenberg (1911:153), Morton (1955) and Peake (1978). The latter author (l. c. p. 507) suggests that there is a minimum viable egg size in land snails, and that there is in small species a

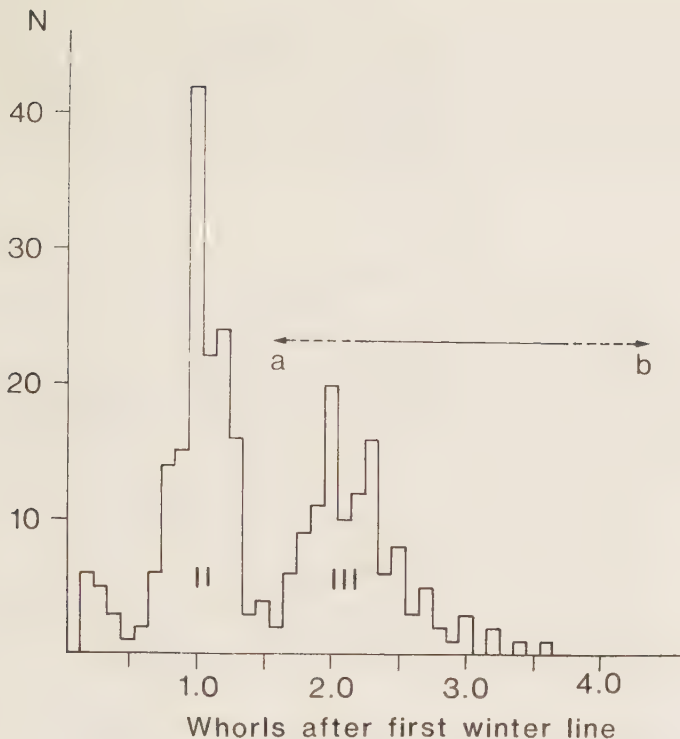


Fig. 2. Lines in shells of *Cochlicopa lubrica* (78 juv. and 96 ad.). The first winter line is placed in origo. II and III = lines from the second and third winter. The mouth-edge of the shell is not marked in the diagram. The animals reach adult stage between a and b. Point a represents a hypothetical snail with an embryonic shell of 1.6 whorls and a maximum observed first year growth of 2.0 whorls and with minimum adult size (5.2 whorls); b represents an animal with minimum first year growth (0.0 whorls) and maximum adult size (5.9 whorls).

protracted egg laying with one or a few eggs laid each time.

C.lubrica seems to fit into this model.

In the present study of C.lubrica there are no data about production and mortality of eggs. The differences in number of juveniles per 10 adults may depend on 1. the sampling technique, which was semiquantitative; 2. different times of sampling; 3. differences in the habitats, and 4. climatic differences between the collection years. From the age distribution it seems as if there sometimes was a heavy mortality among juveniles during their first year of life.

Although Umífski and Focht (1979) based their conclusions on a rather small material, they suggested a juvenile growth period

of 21 - 24 months including two hibernations. Comparing this with the observations from England mentioned above and the results of the present study, it may be concluded that there are great differences in growth rate of C.lubrica in different geographical areas.

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REPRODUCTIVE SUCCESS OF TWO SPECIES OF LAND SNAILS
IN RELATION TO CALCIUM SALTS IN FOREST LITTER

Paper C
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In cultures of Cochlicopa lubrica (Müll.) and Discus rotundatus (Müll.) additions of calcium citrate and calcium oxalate to the substrate had a positive influence on reproduction. The number of juveniles produced could also be increased by sodium carbonate additions. Therefore, both the calcium content and the pH-increasing effect of the calcium compounds in the litter are important.

Ca citrate was more favourable for the snails than Ca oxalate. The oxalate was not decomposed until after 4 - 6 weeks. In feeding experiments it appears to pass unchanged through the alimentary tract of the snails. Leaves of oak, beech and birch as well as the soil-living hyphae of many fungus species are rich in Ca oxalate, while more soluble Ca compounds, e.g. Ca citrate, predominate in leaves of lime, ash, maple and elm. A great fraction of oxalate-bound calcium seems to diminish the accessibility of calcium. pH values are lowered in oxalate-rich forest on non-calcareous bedrock, which probably contributes to the low diversity and low abundance of the snail fauna in such habitats.

INTRODUCTION

A field study of woodland molluscs in southern Sweden intimated that different calcium salts in the leaf litter¹⁾ had different effects upon soil acidity and thereby also on the animals (Wäreborn 1969). The investigation comprised five mollusc habitat types with one locality series in each of them. The habitats were mainly presented by descriptions of the forest types (Wäreborn l. c.p. 466). Applying a recent forest classification (Nordiska Ministerrådet 1980), the forest type, the calcium content in the litter and the soil acidity of each of the five locality series were as follows (cf. also paper E): 1. spruce forest of wet dwarf-scrub-type, with Picea abies (L.): Ca 7.4 ± 0.7 % of ash-free dry weight, pH 4.6 ± 0.1 ; 2. spruce forest of bilberry-type (P.abies, Vaccinium myrtillus L.): Ca 7.7 ± 0.5 %, pH 4.5 ± 0.1 ; 3. oak forest poor in herbs (Quercus spp.): Ca 13.9 ± 0.7 %, pH 5.0 ± 0.2 , and 4. mixed broad leaved forest rich in herbs. The mollusc localities in the latter type were divided into a dry series (Ca 25.9 ± 2.9 %, pH 6.1 ± 0.2) and a moist series (Ca 23.5 ± 1.9 %, pH 6.1 ± 0.3).

Calcium occurs in the three first mentioned habitats to a great extent as calcium oxalate (cf. Mattson and Koutler-Andersson 1946, Linnermark 1960, Hegnauer 1962-1973 and Hintikka et al. 1979). In the two first habitats the humus is of mor type. The oligotrophic oak woods occur on a humus type called moder, inter-

1) partly decomposed litter (sifted material) = foerna (Wäreborn 1969)

mediate between mor and mull. In many species of fungi, occurring in the soil in these three habitats the hyphae accumulate calcium as Ca oxalate (Cromack et al. 1975, 1979, Hintikka et al. 1979). The C/N-quotient is high, the content of polyphenols (tannines) is high, and the plant material has initially rather hard surfaces.

The more nutrient-demanding tree species in the herb-rich deciduous woods are lime (Tilia cordata Mill.), ash (Fraxinus excelsior L.), maple (Acer platanoides L.) and elm (Ulmus glabra Huds.). Their leaves are rich in soluble calcium salts, e.g. Ca citrate and Ca malate. As oak (Quercus robur L.) and to some extent also beech (Fagus sylvatica L.), birch (Betula verrucosa Ehrh.) and hornbeam (Carpinus betulus L.) occur in these woods, Ca oxalate is also present. The C/N-quotient in the litter is lower and the plant material is softer than in the three first mentioned habitats. Soil formation is of mull type. The higher pH values may depend on the higher calcium content but also upon an ample leakage of easily soluble calcium compounds from leaves in the newly fallen litter. Ca is exchangeably adsorbed by the soil or used by e.g. gram-positive bacteria (the gram-negative ones do not accumulate calcium, cf. Davis et al. 1973:92). Bacteria may be an important food source for at least some species of molluscs (Fog 1979).

In the present study the effects of calcium citrate, calcium oxalate and sodium carbonate on the reproductive success of two snail species were investigated. Relations between snails, calcium and pH in forest habitats on non-calcareous bedrock are discussed.

METHODS

Snails of two species, Cochlicopa lubrica (Müll.) and Discus rotundatus (Müll.), were reared in plexiglass boxes under semi-natural outdoor conditions. Calcium-poor leaf litter of beech (F.sylvatica) or oak (Q.robur) was used as substrate in the boxes. A culture comprised 10 snails reared in a box during one season. Four series of cultures were run, viz. a Ca oxalate series, a Ca citrate series, and a series without Ca additions but pH increased by sodium carbonate. For control, a series was kept without additions.

The boxes (28 x 15 x 15 cm) were covered by a plastic net. In the middle part of the bottom the box was open to the ground,

which was covered by hard-packed very calcium-poor soil. This material also surrounded the box in order to enclose the snails, while rain water was allowed to pass down into the ground. The initial calcium content was 10 % of dry weight in the beech-leaf litter and 13 % in the oak litter. The amount of salt added corresponded to 15 % extra calcium.

In order to kill predators the litter was boiled for five minutes in distilled water (or in sodium carbonate solution) before it was placed in the boxes. The content of the boxes was kept moistened by distilled water or, in the sodium carbonate series, by a dilute soda solution during dry weather periods. Eight cultures from different series were as a rule maintained each year. They were started in the middle of June and finished after about 17 weeks. D.rotundatus was reared in oak-leaf and C.lubrica in beech-leaf litter. During the summer the litter was invaded by small soil invertebrates, e.g. springtails, but larger animals, other than the snails, were absent.

The statistical method used for evaluating the results was based upon pairing of the cultures from the same year. If more than one pair of the same series combination could be formed per year, boxes placed close to or near each other were designed to form the pairs.

pH was measured colorimetrically (cf. Wäreborn 1969:463). It changed differently in the box series. When no calcium salt was added, pH increased about one unit during the culture period (from about 5.0 to 6.2). Ca citrate immediately raised pH from 5.0 to about 7.3. Addition of Ca oxalate gave a rise about 4 - 6 weeks after the start of the cultures (from 5.3 to about 7.5). Sodium carbonate kept the pH between 7.0 and 7.8 during the whole culture period.

In order to investigate if snails consume calcium oxalate and if it is taken up from the intestine, specimens of seven species, viz. Cochlicopa lubrica, C.lubricella (Porro), Discus rotundatus, Nesovitrea hammonis (Ström), Aegopinella pura (Alder), Euconulus fulvus (Müll.) and Clausilia bidentata (Ström), were kept for three days on lime-leaf litter covered with small calcium oxalate crystals. Then they were moved individually to separate glass tubes, and their faeces were collected and examined.

RESULTS

The reproduction results are presented in Tab. 1 (D.rotundatus) and Tab. 2 (C.lubrica). The two species reacted in a similar manner to the calcium salts, i.e. with a substantial increase in the number of juveniles. Ca citrate was more favourable for the snails than Ca oxalate ($p < 0.03$ in C.lubrica). This species showed a small but significant increase in reproductive output in boxes with sodium carbonate. The production of C.lubrica juveniles in boxes with calcium salts added was at the same level as at meso- and eutrophic broad leaved forest habitats (cf. paper B).

Juvenile growth of C.lubrica was ≤ 0.8 whorls in boxes with Ca citrate and ≤ 0.9 with Ca oxalate. Observed first year growth maxima under natural conditions were between 1.2 and 2.0 whorls, see paper B. In boxes with no Ca salt additions, i.e. in the sodium carbonate series and in the control series, the growth was ≤ 0.5 whorls.

Corrosion of the adult Cochlicopa shells was least in boxes with Ca citrate and Ca oxalate added. In the control series there was as a rule a heavy corrosion. It was discernibly less in boxes with additions of sodium carbonate.

Examination of the faeces of the abovementioned seven species of snails showed that they had consumed quantities of calcium oxalate crystals. These were unchanged, i.e. their corners were as acute as before feeding and the relation between very small and larger crystals seemed to be about the same as in the original preparation.

DISCUSSION

Previous studies have shown (Künkel 1929, Voelker 1959, Crowell 1973) that addition of calcium carbonate in laboratory experiments directly increases snail reproduction.

The mor-moder-mull syndromes are correlated with the calcium-pH-complex in forest ecosystems. As the leaf substrate was the same in both boxes in all culture box pairs with C.lubrica and D.rotundatus, there are three variables of interest, viz. content of available calcium, pH and microorganism growth on the leaf surfaces. A number of investigated snail species (e.g. D.rotundatus) were able to assimilate 38 - 58 % of the weight of ingested litter leaves (Mason 1970), so microorganisms cannot be the main

TABLE 1

Mean number of juveniles per 10 reared individuals of *Discus rotundatus*.
N = number of cultures.

No calcium added	Calcium added	
	as citrate	as oxalate
3.0 (N=2)	20.3 (N=3)	13.0 (N=2)

TABLE 2

Reproduction of *Cochlicopa lubrica* (Müll.) in cultures with different substrates: A, beech litter without calcium salts added; B, as A, but watered with sodium carbonate solution; C, beech litter mixed with Ca citrate; D, beech litter with Ca oxalate. Significance has been calculated on the mean differences between juvenile numbers in paired samples of culture boxes.

Substrate category	Number of juveniles per 10 adults						Md = mean of differences Significance	
C (with citrate)	15	38	28	38	29	36		
A (no Ca added)	0	6	10	17	7	9	Md = 22.50	t = 8.96
Differences	15	32	18	21	22	27	p < 0.001	
D (with oxalate)	13	21	19	17	25	28		
A (no Ca added)	6	10	7	1	17	7	Md = 12.50	t = 5.84
Differences	7	11	12	16	8	21	p < 0.005	
C (with citrate)	38	17	13	28	38	29		
D (with oxalate)	13	9	6	21	25	25	Md = 10.17	t = 3.31
Differences	25	8	7	7	10	4	p < 0.03	
B (soda watered)	7	15	13	9	9	8		
A (no Ca added)	4	9	10	7	1	4	Md = 4.33	t = 4.71
Differences	3	6	3	2	8	4	p < 0.01	

food of these animals, when they live in the litter. Appropriate calcium compounds in the plant material probably have a direct effect on reproduction. At low calcium levels pH is important for freshwater snails (Økland 1979, cf. also paper D). There may be a direct effect of pH also on terrestrial molluscs (cf. the sodium carbonate series with C. lubrica, Tab. 2). Differences in micro-organism occurrence, correlated with calcium and pH, might, however, contribute to the observed differences in reproduction.

The lower number of juveniles in the Ca oxalate series compared with the number in boxes with Ca citrate added may depend upon the low pH value during the first 4 - 6 weeks and/or on the inability of the snails to utilize oxalate-bound calcium, until it had been broken down by microorganisms. These two causes are probably co-operating (cf. also Økland 1979).

Several kinds of soil microorganisms can decompose Ca oxalate, which recycles the cation and permits formation of calcium bicarbonate. This has a pH-increasing effect. Cromack et al. (1977) have shown that the decomposers mentioned may occur in the intestines of soil animals, though snails were not investigated. According to Hintikka (1979) Ca oxalate decomposers are common and effective: there is not much Ca oxalate left in the H layer. In the overlying L and F layers, however, the oxalate-bound fraction of calcium may be high (about 20 - 40 %). It may amount to > 50 % in beech litter leaves (Mattson and Koutler-Andersson 1946). If there had been a rapid utilization of Ca oxalate in the intestines of the snails, it should have been observed in the feeding experiment. No animals are hitherto known to decompose Ca oxalate in their own tissues (Hodgkinson 1977). A great part of the total calcium content is thus probably not available for the snails, because it occurs in oxalate-bound form in the plant material.

Compared with their normal capacity, juvenile production of the two species studied was low in calcium-poor substrates without additions of calcium salts or sodium carbonate. C. lubrica has a higher constancy than D. rotundatus at the oligotrophic oak wood localities (Wäreborn 1969). The former species is very sparse and the latter is absent in the two spruce forest series. Both species are fairly abundant in the herb-rich deciduous woods. It is inferred that the low abundance or the absence of these two snail species in oligotrophic habitats to great extent is due to low calcium content and low pH values. In acid woodland in south-west

Ireland the abundance of *D.rotundatus* is positively correlated with the calcium content of the litter (Bishop 1977). At more Ca-rich localities in the present study area it is not, in contrast to *C.lubrica*, favoured by calcium (paper E: Tab. 4). *D.rotundatus* has, e.g. in Central Europe, a wide ecological amplitude. In the study area it seems to have less competitive ability than *C.lubrica* (cf. paper E). Both species are probably dependent on a basic level of calcium in suitable chemical form in the litter. They may also be directly affected by low pH values.

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FOOD PREFERENCES AND COMPETITION AMONG SOME

SPECIES OF WOODLAND SNAILS

Paper D

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ABSTRACT

Food preferences and relations to the calcium and pH levels of the environment were investigated experimentally in small woodland species of molluscs. Certain species reacted positively to calcium citrate and to high pH, while others were indifferent. No reactions to calcium oxalate were obtained. This Ca compound, predominating in nutrient-poor habitats, has no direct effect on the pH values.

pH-rising calcium compounds in snail slime can partly neutralize an acid substratum, when the snail is creeping. Calcium content in slime increases towards the autumn, when the new acid-rich litter is incorporated in the woodland snail environment.

Polyphenol content is generally higher in tree leaves from nutrient-poor habitats. *Cochlicopa lubrica* (Müll.) preferred beech litter leaves from a relatively nutrient-rich to beech leaves with the same pH from a nutrient-poor locality, possibly because of a high polyphenol content in the latter leaves. Differences in the film of microorganisms on the leaf surface may also be important.

When tested alone on a relatively calcium-poor leaf litter, most of the snail species preferred lime leaves to leaves of oak and hornbeam. Significant changes in preference, indicating a partial niche differentiation, were obtained when two species were introduced in the same test chamber.

Competitive interactions decreased, when the species were kept on a diet of leaf litter from a more calcium-rich locality. In the field the competition pressure may change seasonally and be critical in late summer, when the amount of leaf litter from nutrient-rich tree species, e.g. lime, decreases considerably.

INTRODUCTION

Spatial distribution of terrestrial molluscs has been related to vegetation (Bishop 1976) and to physical and chemical variables in the environment (Valovirta 1968, Wäreborn 1969 and paper C, Bishop 1977). Moisture, content and state of calcium, and pH have been recognized as important. Other litter and soil components are less well known; while protein, nitrogen and phosphorus appear to be positively influential on most molluscs (Bishop 1977), polyphenols (tannines) are generally negative for soil invertebrates (Edwards and Heath 1975). The content of polyphenols is higher in leaves from trees on nutrient-poor soil (Williams and Gray 1975).

In what extent such environmental factors or complexes of factors govern the food choice of the terrestrial molluscs is unsatisfactorily known. Generally, woodland molluscs are considered to feed mainly on dead plant material (Frömming 1954, Mason 1970, Jennings and Barkham 1975). Although food preferences were reported for a number of mollusc species (Lindquist 1941, Frömming 1954) little is known about what small woodland species really feed on. According to Fog (1979) some species may feed on

bacteria, growing on tree stumps. Similarly, the surface film of microorganisms on leaves in the litter may be important as a food source.

Boycott (1934) stated that among molluscs competition for food is unimportant. This opinion is generally still held (cf. Waldén 1981). There are exceptions concerning a few species, e.g. Harvey (1974) and Carter et al. (1979), who found that competition may be responsible for the distribution pattern of Cepea hortensis (Müll.), C. nemoralis (L.) and Arianta arbustorum (L.).

The unclear picture emerging from extant literature indicates lack of knowledge of two broad fields, viz. food and feeding, and the relations between co-existing species of molluscs, exploiting more or less the same food niche. In this context a number of questions arise, related to the mechanisms acting at the choices of the animals, when they search their way in the litter or to the vegetation to find their food. In the present study it is tried to shed light on some of these questions by testing a number of woodland snail species for reactions to differences in environmental variables with particular reference to the food selection of the animals.

MATERIAL AND METHODS

For the tests, adults and large juveniles of the following species were used: Carychium tridentatum (Risso), Cochlicopa lubrica (Müll.), C. lubricella (Porro), Vallonia costata (Müll.), Acanthinula aculeata (Müll.), Discus rotundatus (Müll.), Nesovitrea hammonis (Ström), Aegopinella pura (Alder), A. nitidula (Drap.) and Trichia hispida (L.). Most of the snail material was collected in herch-rich broad leaved woods on non-calcareous bedrock in southern Sweden. The specimens of N.hammonis were from oligotrophic forest (Picea, Fagus, Quercus). The material of C.lubrica, V.costata and T.hispida was collected in deciduous woods in calcareous areas. The snails were collected about a week before the tests and kept in mixed leaf litter on moistened vermiculite.

For tests of reactions to calcium and pH, straight chambers with eight compartments containing calcium-poor beech leaf litter were used (cf. Lindroth 1949). In every second section 100 mg calcium citrate powder was added. Two, four or eight test animals were used per section. The chamber was darkened and kept at 16°C

in the laboratory for 2-3 days; then the position of the animals was registered. Two parallel experiments were made with most of the species. Tests with calcium oxalate were made in the same way. The litter used in the chambers had a pH about 5.5. Ca citrate increased pH in the litter about one unit, while Ca oxalate had no direct effect on acidity.

pH tests with buffer solutions were made in a shallow chamber without sections (390 x 43 x 7 mm). The bottom was covered with eight squares of filter paper, placed with interspaces of 0.5 mm and soaked with buffers of different pH. At the first experiments a 0.033 M acetate buffer was used, while an investigation of a possible effect of the citrate ion per se was carried out with a 0.050 M citrate buffer and a 0.033 M phosphate buffer, both with pH 6.6.

An early series of preference tests with various kinds of leaf litter was carried out in a circular gradient chamber subdivided in ten sections. After the recognition of competitive interference (cf. paper E) the method was changed as follows. In dishes of glass (diameter 15 cm) a thin layer of moistened vermiculite covered the outer parts of the bottom. On this layer were placed three packets of litter leaves from different species of trees. Between the packets, each of which consisted of only two leaves, there was a distance of about 5 cm. The dish was covered with a perforated plastic sheet. The test animals were placed in the free area in the middle of the dishes. These were then kept dark in an openly ventilated cellar room at a diel temperature gradient of 12 - 16°C (occasionally 9 - 17°C). The position of the animals was registered after 12 hours. Each such series consisted of 10 tests.

The feeding efficiency differed between the species investigated. Specimens of Cochlicopa lubricella rapidly cleaned the surface of a pair of lime litter leaves. They ate much of the epidermis (also on the veins), and after one or two days they switched to their second preferred food. Therefore, the leaves were changed after each test with this species. Otherwise, they were exchanged after 3 - 4 tests together with the vermiculite, which in a few days developed a bacterial flora, that apparently attracted the snails.

Within the same experiment or test series the statistical analyses were performed on paired samples. Ordinary t-tests have been used to analyse particular differences between different

series. Differences between whole experiment series have been analysed with chi-square tests.

RESULTS

SIGNIFICANCE OF CALCIUM IONS AND pH

Discus rotundatus and Carychium tridentatum reacted positively to Ca citrate: D.rotundatus (four test animals per section, $n = 64$): control $\bar{x} = 1.5$, with Ca citrate $\bar{x} = 6.5$, $p < 0.005$; and C. tridentatum (eight animals per section, $n = 64$): control $\bar{x} = 6.0$, with Ca citrate $\bar{x} = 10.0$, $p < 0.05$. No significant results were obtained with Cochlicopa lubrica, Trichia hispida, Vallonia costata and Nesovitrea hammonis. This was not due to insufficient motility of the specimens.

D.rotundatus and C.lubrica did not react to Ca oxalate additions to beech-leaf litter. C.lubrica did not react after the pH of the litter had been artificially raised in every second compartment with a weak sodium carbonate solution.

In the pH experiments on filter paper there was a significant reaction of D.rotundatus (four animals per section, $n = 64$): pH 5.0: $\bar{x} = 0.4$, pH 6.5: $\bar{x} = 4.6$, $p < 0.01$. Animals which had ascended the lid and the sides of the chamber were not included. T. hispida and C.lubrica did not react in these experiments. N.hammonis showed a weak tendency to choose the lower pH value. The clear preference of D.rotundatus for sections with high pH values agrees with its positive reaction to Ca citrate. It should be remembered, however, that the test animals came from localities with more or less the preferred pH values, and that a change in pH also means other changes in the chemical composition of the buffer solution.

The effect of the citrate ion, occurring in calcium citrate, was studied separately (besides from its pH effect). Specimens of D.rotundatus were allowed to choose between a citrate buffer and a phosphate buffer, both with pH 6.6, but no significant result was obtained.

It is easily demonstrated that snails produce pH-rising substances in slime. Specimens of Nesovitrea hammonis, Aegopinella pura and A.nitidula were placed on moistened special indicator paper (Merck 9556). A rise of 0.5 - 1.0 unit was obtained. It is known (Kühnelt 1932, Dexheimer 1953) that snail slime has a high

Ca content. It might also be suspected that excretion of ammonia could be responsible for the pH increase (Loest 1979). These possibilities were tested by placing three specimens of N.hammonis and the same number of A.pura on films of citrate buffer solution with pH 4.3 for three minutes. Tests with ammonium oxalate showed that both species excrete calcium in slime in the described situation. Tests with Nessler's reagent for ammonia in parallel experiments gave negative results.

FOOD PREFERENCES AND SPECIES RELATIONS

In a circular gradient chamber leaf litter of beech (Fagus sylvatica L.) from an oligotrophic locality was placed in odd sections, while the even ones were filled with litter from the same tree species from a mesotrophic locality (E 10, cf. Wäreborn 1969 and paper E). The pH was about the same in the two leaf samples. When C.lubrica (n = 50) was introduced to the chamber, a significant ($p < 0.02$) difference in distribution was obtained. Twenty-four percent of the snails were found in the oligotrophic litter and 76 % in the litter from the nutrient-richer locality. The test animals came, however, from a trophically favourable wood habitat, which may have affected the outcome of the experiment.

Food preferences of N.hammonis and A.pura were tested in glass dishes with a choice of litter leaves from lime (Tilia cordata Mill.), oak (Quercus robur L.) and hornbeam (Carpinus betulus L.), collected at a mesotrophic locality (D 49). The results are presented in Tab. 1. Chi-square tests showed that the difference between the whole distributions in the single species experiments with N.hammonis and with A.pura and the differences between single and two-species experiments with the same two species were significant. A.pura significantly preferred lime leaves to hornbeam and oak. In two-species experiments N.hammonis exploited hornbeam leaves more than A.pura ($p < 0.005$). The latter species had a greater tendency to roam about beside the litter leaves than N.hammonis ($p < 0.005$ and $p < 0.001$).

C.lubricella was tested single and together with A.pura. When alone, C.lubricella (n = 10 - 11) preferred lime leaves very clearly ($p < 0.001$, cf. Fig. 1). In connection with A.pura (n = 10 + 10), C.lubricella lost its dominating exploitation of the lime litter (from D 49) to A.pura, which increased its choice of

TABLE 1

Food preferences of *Nesovitrea hammonis* and *Aegopinella pura*, single and in combination. n = number of test animals, $\bar{x}$ = mean number in a test series and s = standard deviation.

A. Single species

Col. No.	<i>N.hammonis</i> (n = 20) Leaf litter from				<i>A.pura</i> (n = 20) Leaf litter from			
	lime	oak	horn-beam	beside leaves	lime	oak	horn-beam	beside leaves
	1	2	3	4	5	6	7	8
	4	7	7	2	7	8	3	2
	6	6	7	1	5	5	7	3
	3	6	7	4	5	4	9	2
	10	6	2	2	7	8	2	3
	7	10	3	0	11	2	3	4
	6	6	5	3	6	1	4	9
	8	7	5	0	13	3	0	4
	12	6	2	0	6	5	1	8
	11	6	2	1	10	4	1	5
	9	4	4	3	6	4	1	9
$\bar{x}$	7.6	6.4	4.4	1.6	7.6	4.4	3.1	4.9
s	2.95	1.51	2.12	1.43	2.76	2.27	2.88	2.77

B. Two species in combination

Col. No.	<i>N.hammonis</i> (n = 20) lime oak horn-beam beside leaves				<i>A.pura</i> (n = 20) lime oak horn-beam beside leaves			
	9	10	11	12	13	14	15	16
	8	3	6	3	13	2	2	3
	6	3	7	4	8	2	1	9
	9	2	5	4	5	5	5	5
	3	2	12	3	7	3	3	7
	2	7	7	4	7	3	2	8
	7	7	2	4	8	3	1	8
	6	5	7	2	9	0	1	10
	10	9	1	0	9	3	1	7
	5	7	6	2	7	2	3	8
	7	3	8	2	10	5	1	4
$\bar{x}$	6.3	4.8	6.1	2.8	8.3	2.8	2.0	6.9
s	2.50	2.53	3.07	1.32	2.16	1.48	1.33	2.23

Significances: The difference between the distributions in the single species experiments with *N.hammonis* and with *A.pura* was significant ($\chi^2 = 78.15$ $p < 0.001$) as well as the differences between single and two-species experiments with the same two species ($\chi^2 = 21.79$, $p < 0.001$; $\chi^2 = 18.73$, $p < 0.001$). Other significances:

a) t-test, unpaired samples:
column No. 4) and 8) $p < 0.005$

b) tests on paired samples:
column No. 5) and 6) $p < 0.05$
5) and 7) $p < 0.005$
11) and 15) $p < 0.005$
12) and 16) $p < 0.001$
13) and 14) $p < 0.001$
13) and 15) $p < 0.001$

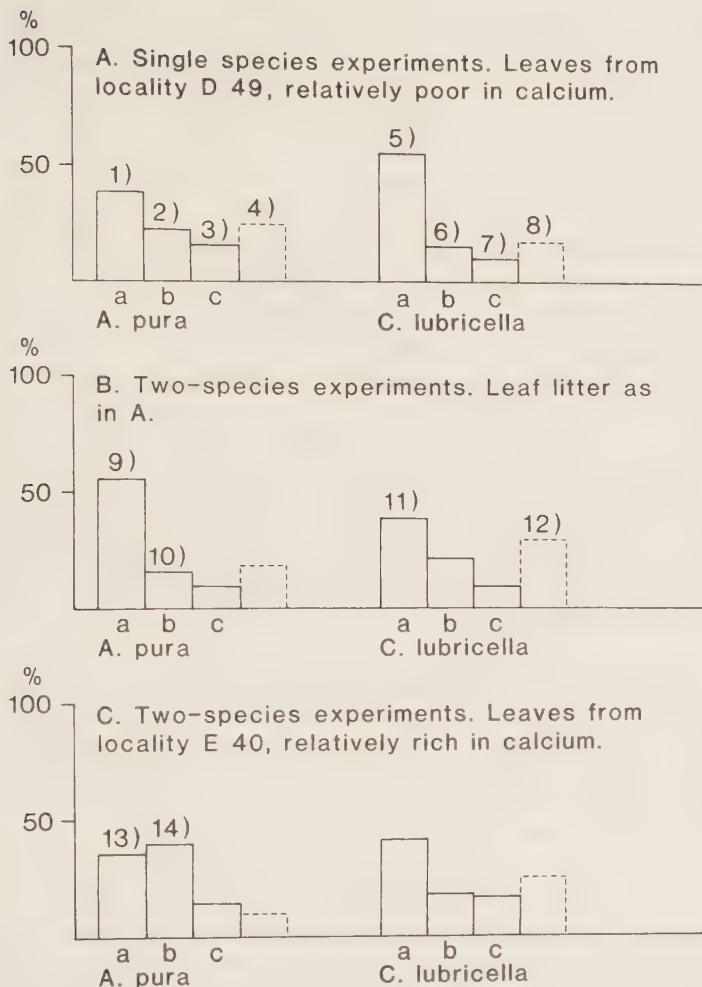


Fig. 1. Preference experiments with *Aegopinella pura* and *Cochlicopa lubricella* on leaf litter from herb-rich deciduous wood localities. a = lime-leaf litter, b = oak-leaf litter, and c = litter from hornbeam. Dotted lines = animals found beside the leaf litter. Each bar in the diagram represents an average from 10 experiments with 10 (11) animals. The differences in the *A. pura* and *C. lubricella* distributions between single and two-species experiments were significant ($\chi^2 = 12.43$, $p < 0.01$ and $\chi^2 = 15.22$, $p < 0.005$). This was also true of the difference between the *A. pura* distributions on Ca-poor and on Ca-rich litter ($\chi^2 = 43.48$, $p < 0.001$). Other significances:

a) tested on paired samples	b) t-tests, unpaired samples
1) and 9) $p < 0.05$	1) and 9) $p < 0.02$
1) and 3) $p < 0.005$	5) and 11) $p < 0.01$
5) and 6) $p < 0.001$	8) and 12) $p < 0.05$
5) and 7) $p < 0.001$	9) and 13) $p < 0.02$
	10) and 14) $p < 0.001$

this kind of litter considerably. The changes are significant in both species. The tendency of C.lubricella to roam about beside the litter increased significantly, when A.pura was present. As the test chambers were treated in the same way, the difference was probably not caused by differences in bacterial growth on the vermiculite.

The same pair of snail species ($n = 10 + 10$) were also tested on litter leaves from a more calcium-rich locality (E 40). The results are presented in Fig. 1. The food preferences were less pronounced in both species. In A.pura the preference decreased ($p < 0.02$) for lime leaves but increased ($p < 0.001$) for oak leaves compared with the tests on calcium-poor litter. The dominating exploitation of lime litter, shown by this species on calcium-poor leaves, disappeared. In C.lubricella there were no significant changes, though hornbeam leaves appeared to be somewhat more acceptable (cf. Fig. 1). The total differences in A.pura and C.lubricella between single and two-species experiments and the total difference between the distributions of A.pura on Ca-poor and Ca-rich litter were significant (chi-square tests, cf. Fig. 1).

Nine specimens of Acanthinula aculeata were tested on litter from D 49 in a series of ten repetitions. Forty-three percent were found on lime leaves, 32 % on oak and 20 % on hornbeam. The difference between lime and hornbeam is significant ($p < 0.02$).

DISCUSSION

Food choice of terrestrial molluscs is affected by several factors. Many soil invertebrates react negatively to polyphenols (Edwards and Heath 1975). In the experiments, C.lubrica preferred beech-leaf litter from a nutrient-rich to the same kind of litter with the same pH from a nutrient-poor locality; this might depend on differences in polyphenol content. Other substances with deterring actions on snails probably occur (Grime et al. 1968). It was also reported that snails may be attracted by odours from food substances (Croll 1980).

Calcium occurs to great extent as Ca citrate in leaves of nutrient-demanding trees, e.g. in lime (Hegnauer 1962-1973), while Ca oxalate is dominating e.g. in oak, beech, hornbeam and birch (*Betula* spp.). In the experiments with calcium citrate two species reacted positively. A test was made on the citrate ion

separately. As no significant reaction was obtained, the animals probably react to the pH-rising effect of the Ca citrate. Tests on calcium oxalate with two snail species gave no significant results, i.e. the animals did not avoid this salt (cf. Lindquist 1941). The snails probably do not utilize it directly, but when broken down by microorganisms, it may be an important Ca source (cf. paper C).

Different reactions to pH differences have been obtained. According to Fog (1979) Iphigena plicatula (Drap.) avoids low pH values; other species studied by him were indifferent to pH. In the present study some species did not react, while D. rotundatus preferred a pH value of 6.5 to pH 5.0. Species attracted by a high pH may stay and feed on litter leaves rich in suitable calcium compounds, e.g. Ca citrate. These leaves may also be recognized by low content of polyphenols and/or by odour and surface texture (cf. Grime et al. 1968). Differences in the surface film of microorganisms probably correlated with pH, calcium and polyphenol content may also be important (cf. Fog 1979).

The physiological system of the molluscs is more or less open to the environment. Direct chemical interrelations are found between freshwater snails and water chemistry, e.g. the animals use the calcium supply in their bodies to raise a low calcium content and a low pH in the water (Thomas et al. 1974, Thomas and Lough 1974). This is possible, when the water volume per snail is relatively small. Freshwater snails can endure lower pH values, when calcium concentrations are not too low (Økland 1979). In Helix pomatia (L.) there is a supply of calcium carbonate in the sole, near the main slime-producing gland (Burton 1976). Towards the autumn the calcium content increases in the slime, and this has been interpreted (Dexheimer 1953) as a preparation for the winter epiphragm. But all molluscs do not produce epiphragms, so the main reason for the increase of calcium in slime may simply be to neutralize acid substances in the acid-rich new litter in autumn (cf. Mattson and Koutler-Andersson 1954). Accordingly, individuals of species with ability to accumulate sufficient calcium from a relatively calcium-poor food may be able to partly neutralize the acid substratum where they are creeping and thus better endure low pH values. These may affect e.g. shell corrosion (cf. paper C).

Contrary to the present results, Fog (1979) found that D. rotundatus did not react against low pH, when exploiting bacterial

films on tree stumps. The reason might be that there was no lack of calcium in his study area and/or that the animals were more attracted by the food than they were deterred by the low pH. I.plicatula preferred gram-negative bacteria, which are poor in calcium (Davis et al. 1973:92). Possibly therefore, it avoided stumps with low pH values.

Although a species does not react to pH differences, its reproduction may be affected by a low pH level (C.lubrica, cf. paper C).

Cochlicopa lubrica, C.lubricella, Aegopinella pura and Acanthinula aculeata showed clear food preferences in the single species experiments. Nesovitrea hammonis exploited the litter leaves tested more evenly.

In the two-species tests with a relatively calcium-poor leaf litter the preferences were changed, which indicates a partial niche differentiation. Between A.pura and C.lubricella there seems to be a competitive interference on this litter. N.hammonis and A.pura differed in their exploitation of hornbeam leaves. In the experiments with a more calcium-rich litter competition seemed to decrease, and both species accepted a variety of litter leaves. There may in relatively calcium-poor woodland habitats be a calcium-related interspecific food competition. Towards the end of the summer the amount of leaves from lime, ash (Fraxinus excelsior L.), maple (Acer platanoides L.) and elm (Ulmus glabra Huds.) decreases considerably in the litter in relation to oak and beech leaves (cf. Nordström and Rundgren 1974); at this period competition may be critical for some mollusc species.

If a species is prevented from taking its preferred food, the growth may be restricted and as a consequence the reproduction impaired (Oosterhoff 1977, and Carter et al. 1979, on Cepaea species).

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ENVIRONMENTS AND MOLLUSCS IN A NON-CALCAREOUS FOREST AREA
IN SOUTHERN SWEDEN; WITH REMARKS ON COMPETITION AMONG
TERRESTRIAL SNAILS

Paper E
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In a field study of woodland molluscs there was an important fauna distinction between forests on soils with humus of mor and moder type and forests on soils with humus of mull type. Snail abundance and species numbers of molluscs were both correlated with calcium content in the litter in oligotrophic forest types. Soil acidity was correlated with the calcium content. It is also related to the chemical form of the existing calcium and to other environmental variables. The pH values *per se* probably have an effect on molluscs at low pH and calcium levels. Soil moisture is important for the molluscs and also sun exposure, which affects air humidity.

Snail distributions, indicating effects of interspecific competition, were observed. In mixed herb-rich deciduous wood there was a group of species, which mainly occurred at relatively calcium-poor localities. These species occur elsewhere in very calcium-rich habitats. Some other species with a wide ecological amplitude and occurring in all forest types in the area, reached high abundance in the herb-rich deciduous woods at sun-exposed localities, where there might be a decreased competition pressure from drought-sensitive species.

INTRODUCTION

A field study of molluscs was performed in an oligotrophic forest area in southern Sweden (Wäreborn 1969). Conifers predominated; at places there were oak woods and relatively eutrophic deciduous woods. The latter were as a rule situated on the slopes of greenstone ridges. There was no limestone in bedrock or in moraine.

The localities studied were situated in four types of forests: spruce forest of wet dwarf-scrub-type (= moist mixed wood in Wäreborn 1969), spruce forest of Vaccinium myrtillus type (= drier mixed wood), oak forest of herb-poor type (= oligotrophic oak wood), and mixed, broad leaved forest of herb-rich type (= meadow wood). As the localities in the latter forest type were divided into a moist and a drier series on the basis of soil moisture, there were five locality series corresponding to five different types of mollusc habitats. Each series consisted of 10 - 12 localities. The forest types are here classified according to Nordiska Ministerrådet (1980).

The volumetric sampling method chosen allowed exploration of especially favourable litter- and snail-rich patches within the 10 x 20 m sample areas. In six of the herb-rich deciduous wood localities a parallel sampling in squares (50 x 50 cm) was carried out. The sample volume (3.0 l), used in the main method, corresponded to $1.5 \pm 0.3 \text{ m}^2$ of soil surface in these woods.

An important fauna distinction was found between the herb-rich deciduous wood habitats and the others (cf. Tab. 1 in this

TABLE 1

Distribution of molluscs between different habitat types. A = moist spruce forest, B = drier spruce forest, C = oligotrophic oak wood, D = drier herb-rich deciduous wood, and E = moist herb-rich deciduous wood. Mi = average individual number/locality, recalculated to correspond to 3.0 l after sifting (cf. Wäreborn 1969:462). C = constancy.

A few corrections have been made in the oak wood series in relation to Wäreborn 1969: loc. 78 and loc. 54: five and two specimens of *C. lubrica* should be *C. lubricella*, loc. 71: one specimen of *V. substriata* should be *V. alpestris*.

Habitat series Number of localities	A 10		B 11		C 10		D 12		E 12	
Species	Mi	C%	Mi	C%	Mi	C%	Mi	C%	Mi	C%
<i>Punctum pygmaeum</i> (Drap.)	1	30	0.1	9	13	100	60	100	127	100
<i>Nesovitrea hammonis</i> (Ström)	37	100	29	100	62	100	69	100	52	100
<i>Euconulus f. fulvus</i> (Müll.)	14	100	10	100	27	100	44	100	44	100
<i>Cochlicopa lubrica</i> (Müll.)	0.3	20	—	—	3	70	13	100	32	100
<i>Vertigo substriata</i> (Jeffr.)	3	80	3	82	8	80	8	100	25	100
<i>Nesovitrea petronella</i> (Pfeiffer)	—	—	—	—	—	—	14	67	27	92
<i>Columella aspera</i> Waldén	4	100	9	100	12	100	13	100	15	92
<i>Clausilia bidentata</i> (Ström)	1	30	0.2	9	3	30	11	100	10	92
<i>Carychium tridentatum</i> (Risso)	—	—	—	—	—	—	55	50	197	83
<i>Discus rotundatus</i> (Müll.)	—	—	—	—	1	20	19	92	9	83
<i>Vertigo pusilla</i> Müll.	—	—	—	—	—	—	2	58	3	75
<i>Discus ruderatus</i> (Hartm.)	1	20	2	45	1	30	6	83	4	67
<i>Vitrina pellucida</i> (Müll.)	—	—	—	—	0.3	30	1	58	3	67
<i>Cochlicopa lubricella</i> (Porro)	—	—	—	—	0.7	20	5	58	42	58
<i>Vitrea contracta</i> Westerl.	—	—	—	—	0.1	10	2	42	7	58
<i>Cepaea hortensis</i> (Müll.)	—	—	—	—	0.1	20	1	92	1	58
<i>Helicigona lapicida</i> (L.)	—	—	—	—	—	—	1	42	1	42
<i>Vitrea crystallina</i> (Müll.)	—	—	—	—	—	—	21	50	11	33
<i>Aegopinella pura</i> (Alder)	—	—	—	—	—	—	12	58	9	33
<i>Bradybaena fruticum</i> (Müll.)	—	—	—	—	0	10	0.3	25	2	33
<i>Oxychilus alliarius</i> Mill.	1	40	1	18	0.1	20	1	25	1	33
<i>Cochlodina laminata</i> (Mont.)	—	—	—	—	—	—	3	42	2	25
<i>Arianta arbustorum</i> (L.)	—	—	—	—	0	20	0.4	50	0.3	25
<i>Trichia hispida</i> (L.)	—	—	—	—	—	—	0	8	11	17
<i>Columella edentula</i> (Drap.)	—	—	—	—	—	—	—	—	2	17
<i>Iphigenia plicatula</i> (Drap.)	—	—	—	—	—	—	1	33	0.3	17
<i>Vertigo alpestris</i> Alder	—	—	—	—	0	10	—	—	0.3	17
<i>Vallonia excentrica</i> Sterki	—	—	—	—	—	—	0	17	0.1	17
<i>Aegopinella nitidula</i> (Drap.)	—	—	—	—	—	—	0.1	8	1	8
<i>Acanthinula aculeata</i> (Müll.)	—	—	—	—	—	—	4	33	1	8
<i>Vertigo pygmaea</i> (Drap.)	—	—	—	—	—	—	—	—	0.1	8
<i>V. romneyensis</i> (Westerl.)	—	—	2	27	—	—	—	—	—	—
Number of snails per locality, average..	62		56		130		367		634	
Number of species, slugs included.....	12		15		22		37		40	

paper). Most mollusc species had a much higher abundance in the relatively eutrophic woods. There were in these almost twice as many species as in the three oligotrophic forest habitats. Independently of the difference in bedrock, there seemed to be a positive effect of the slope situation on vegetation and molluscs (cf. Waldén 1981). In the moist spruce forest there was a fairly abundant admixture of Betula pubescens Ehrh. and Salix spp. The oak woods still had a much better supply of deciduous leaf litter than the two types of spruce forest. Habitat differences between the five locality series comprised major differences in litter decomposition and soil formation (mor, moder and mull type, cf. paper C).

The mollusc occurrence was related to environmental variables, e.g. calcium, pH and moisture. In the calculations, the calcium content was related to the dry weight of the analysed material, i.e. the sift samples from the L and F layers in oligotrophic soils and from the L and upper parts of the A_1 layer in soils of herb-rich deciduous woods (mesh width of sieve: 0.9 cm). Analyses were also made of samples of mineral soil (or peat in the moist spruce forest). Significant correlations between the abundance of snails and the calcium content of the litter were presented for the moist spruce forest series and the oligotrophic oak wood series (Wäreborn 1969:469, 471). In the drier herb-rich deciduous wood series there was a correlation between snail abundance and soil moisture (ibid. p. 476).

Within the 24 localities in the herb-rich deciduous woods three locality sub-groups (I - III) were discerned at the basis of snail fauna similarities (Wäreborn 1969:477). The same localities were also preliminarily grouped into a calcium-poor and a calcium-rich series (ibid. p. 476). The results, as regards the distribution of some species of snails in relation to calcium, were not quite consistent with other observations in southern Sweden. This applies especially to Carychium tridentatum, which probably is favoured by a high calcium content (Waldén 1969).

In cultures of two snail species, additions of calcium citrate, calcium oxalate and sodium carbonate had positive effects on reproduction. Calcium citrate was best for the snails. The Ca oxalate was probably not utilized until it had been broken down by microorganisms. The pH values per se seemed to have an effect on the reproductive output (paper C).

A study of food preferences indicated that food competition occurs among woodland snails (paper D). Since Boycott (1934) it is generally accepted (cf. Waldén 1981) that competition for food is of minor importance among terrestrial molluscs. Evidence

of interspecific competition was, however, presented in a few cases, e.g. Waldén (1969) in Oxychilus; Harvey (1974), Cameron & Carter (1979), and Carter et al. (1979) in Arianta and Cepaea. Food quality may be crucial for molluscs. Appropriate food is needed for optimal growth, which at least in Cepaea spp. is correlated with successful reproduction. Effects of activity-inhibiting pheromones in the slime of two Cepaea species have been reported (Cameron and Carter 1979). This may be a mechanism of competitive interference, preventing depletion of essential food resources.

It was demonstrated (Sjörs 1971) that the conventional method of calculating calcium content gives very low values in soils of mull type, because of the high mineral content. The calculations should be made on ash-free dry weight. Calcium is thereby related to the organic content of the analysed material and to the food of the molluscs. This method has been applied in the present study, which is a further analysis of the data in Wäreborn 1969. It was aimed at investigating the importance of the calcium-pH-complex for woodland molluscs in relation to other environmental factors.

RESULTS

SPECIES NUMBERS AND SNAIL ABUNDANCE IN RELATION TO CALCIUM AND pH

Recalculated values of calcium in litter show a much higher calcium content in relation to ash-free dry weight in herb-rich deciduous wood than in oligotrophic oak wood (Tab. 2, cf. Wäreborn 1969:470).

The significant correlations between snail abundance and calcium content in the litter in the moist spruce forest and in the oak wood persist also when calcium is calculated relative to ash-free dry weight (Fig. 1). The correlation coefficient is slightly lowered in the former habitat. In the oak woods there is a closer correlation and there is a much more plausible slope of the regression line than before recalculation. This line is now almost parallel to the regression line in the moist spruce forest.

Relations between total number of mollusc species and calcium content in the litter are illustrated in Fig. 2. In the three oligotrophic series the species numbers seem to depend partly on calcium in the habitat, while in the herb-rich deciduous wood the species numbers probably are regulated by other factors.

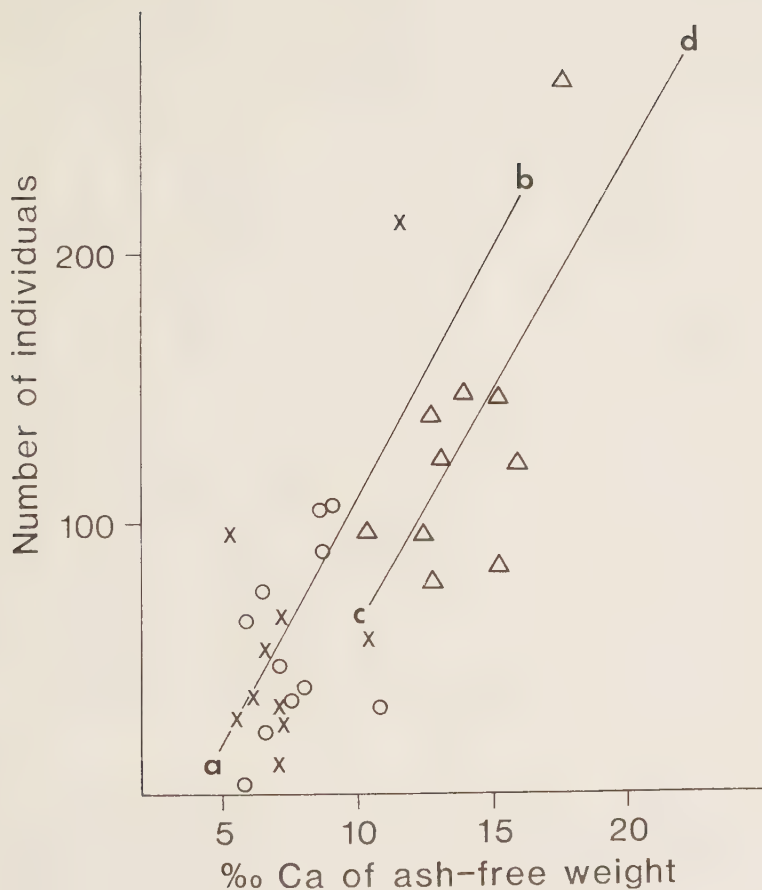


Fig.1. Numbers of snails in relation to Ca content of the litter (x= the moist spruce forest locality series, O= the drier spruce forest series, and Δ = the oligotrophic oak wood series). The individual numbers correspond to a sample volume of 3.0 l. The regression line a - b, $y = 18.5x - 75.7$, $r = 0.640$, $p < 0.05$, refers to the moist spruce forest series and the line c - d, $y = 17.3x - 110.5$, $r = 0.680$, $p < 0.05$, to the oak wood series. No significance was found in the drier spruce forest series, but taken together the three series show a highly significant correlation ($r = 0.741$, $p < 0.001$). Its regression line ($y = 12.4x - 37.4$) is not drawn in the figure.

TABLE 2

Calcium in litter, related to ash-free dry weight. A: localities in moist spruce forest, B: in drier spruce forest, C: in oligotrophic oak wood, D: in drier herb-rich deciduous wood, and E: in moist herb-rich deciduous wood. O. = organic content. $\bar{x}$ = average calcium content of the locality series, given with standard error. For locality descriptions, see Wäreborn 1969.

A.			B.			C.			D.			E.		
Loc. No.	O. %	Ca ‰	Loc. No.	O. %	Ca ‰	Loc. No.	O. %	Ca ‰	Loc. No.	O. %	Ca ‰	Loc. No.	O. %	Ca ‰
61	96	5.3	53	96	5.9	74	53	10.3	39	41	17.0	10	40	18.3
75	96	5.6	50	96	6.0	79	43	15.2	68	28	42.1	16	63	18.6
62	95	6.2	57	88	6.6	66	59	12.3	33	38	18.7	44	38	23.7
63	94	6.6	55	95	6.6	78	56	13.2	12	50	20.7	67	31	20.6
80	94	7.1	21	93	7.1	77	71	12.6	37	79	16.4	42	33	27.8
81	93	7.2	43	94	7.5	65	69	13.9	34	18	34.6	38	31	29.3
76	96	7.1	52	95	8.0	51	68	15.1	49	32	20.6	45	42	21.0
64	96	7.2	36	92	8.8	54	86	12.7	9	47	18.3	31	40	22.1
72	96	10.4	46	96	8.7	71	91	15.9	30	31	35.4	70	46	18.6
59	96	11.6	48	94	9.1	20	84	17.7	35	32	21.6	41	41	37.8
			56	92	10.8				47	56	23.1	40	41	29.0
									32	27	42.7	13	86	14.7
$\bar{x} = 7.4 \pm 0.7$			$\bar{x} = 7.7 \pm 0.5$			$\bar{x} = 13.9 \pm 0.7$			$\bar{x} = 25.9 \pm 2.9$			$\bar{x} = 23.5 \pm 1.9$		

After calculation of calcium relative to ash-free dry weight of the analysed material new calcium-poor and calcium-rich series were formed (Tab. 4, cf. Wäreborn 1969:476). The abundance of snails seems to be considerably higher in the Ca-rich series, while the species numbers of molluscs are almost equal.

The abovementioned three locality sub-groups within the herb-rich deciduous wood habitat have been submitted to a further analysis (Tab. 4). It was found that all the localities of group I fell into the new calcium-poor series. All the localities of group III except two fell into the new calcium-rich series. The localities of group I and III were relatively shady. The group II localities showed a fairly high average content of calcium. They were distinctly more open and sun-exposed than the others. The differences in calcium content were statistically significant.

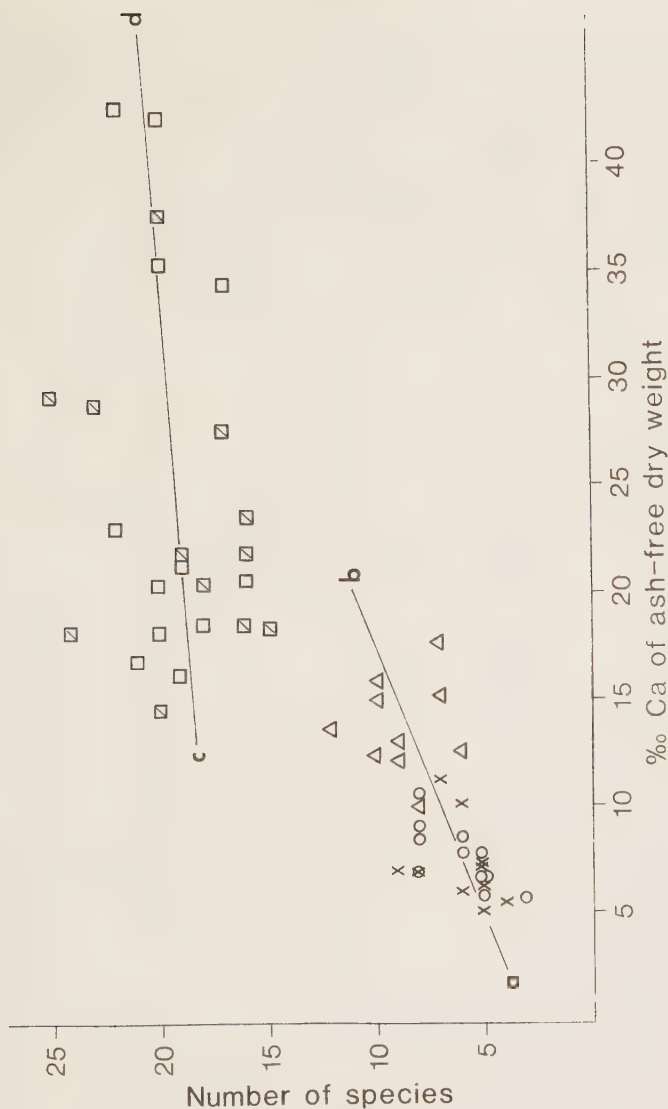


Fig. 2. Total number of mollusc species per locality in relation to Ca content of the litter (x = the moist spruce forest series, O = the drier spruce forest series, Δ = the oligotrophic oak wood series, ◻ = the drier herb-rich deciduous wood series, and ◻ = the moist herb-rich deciduous wood series). The regression line a - b, $y = 0.395x + 3.13$, $r = 0.662$, $p < 0.001$, refers to the three first mentioned series and the line c - d, $y = 0.075x + 17.45$, $r = 0.22$, n. s., to the two herb-rich deciduous wood series.

TABLE 3

Distribution of molluscs between different pH classes in relation to the calcium content of the most calcium-poor locality. The table presents average individual numbers per locality, recalculated to correspond to a volume of 3 l after sifting (cf. Wäreborn 1969:462). + = shells from dead snails. Ca_{min} = calcium content of the litter (% of ash-free weight) at the most calcium-poor locality of the species. Numbers within brackets are based upon ≤ 5 localities.

Number of localities		18	17	17	3	
Species	pH	≤ 4.5	4.6-5.5	5.6-6.5	>6.5	Ca _{min} .%
<i>Punctum pygmaeum</i>		2.7	18.8	94.9	134.7	7.1
<i>Nesovitrea hammonis</i>		37.2	47.0	69.3	32.3	3.7
<i>Euconulus fulvus</i>		12.6	24.4	49.6	35.0	3.7
<i>Cochlicopa lubrica</i>		0.3	5.3	24.5	21.0	6.6
<i>Vertigo substriata</i>		3.9	7.3	14.7	34.0	5.3
<i>Nesovitrea petronella</i>		-	4.2	18.7	33.7	14.7
<i>Columella aspera</i>		6.8	9.8	15.3	12.3	5.3
<i>Clausilia bidentata</i>		1.1	1.8	10.8	16.3	6.2
<i>Carychium tridentatum</i>		-	9.7	147.0	119.7	14.7
<i>Discus rotundatus</i>		0.7	5.1	13.8	5.7	13.9
<i>Vertigo pusilla</i>		-	0.5	2.1	3.0	14.7
<i>Discus ruderratus</i>		0.8	2.5	4.9	6.7	3.7
<i>Vitrina pellucida</i>		0.1	0.2	2.0	3.7	12.6
<i>Cochlicopa lubricella</i>		0.4	2.2	14.7	93.0	17.0
<i>Vitrea contracta</i>		-	1.2	3.7	7.0	15.2
<i>Cepaea hortensis</i>		+	+	1.2	1.0	13.9
<i>Helicigona lapicida</i>		-	0.2	0.9	2.3	14.7
<i>Vitrea crystallina</i>		-	4.9	16.5	3.0	14.7
<i>Aegopinella pura</i>		-	2.8	7.4	21.7	14.7
<i>Bradybaena fruticum</i>		-	+	0.9	2.7	22.1
<i>Oxychilus alliarius</i>		0.4	0.6	0.5	1.3	5.6
<i>Cochlodina laminata</i>		-	1.4	1.3	5.7	14.7
<i>Arianta arbustorum</i>		-	0.3	0.2	+	12.3
<i>Trichia hispida</i>		-	-	1.9	31.0	(18.3)
<i>Columella edentula</i>		-	0.2	1.3	-	(18.3)
<i>Iphigena plicatula</i>		-	0.4	0.9	-	17.0
<i>Vertigo alpestris</i>		+	-	0.1	0.7	(15.9)
<i>Vallonia excentrica</i>		-	-	0.1	+	(23.1)
<i>Aegopinella nitidula</i>		-	0.9	0.1	-	(18.3)
<i>Acanthinula aculeata</i>		-	0.8	2.5	-	(17.0)
<i>Vertigo pygmaea</i>		-	-	-	0.3	(37.8)
<i>Vertigo ronneyensis</i>		1.0	-	-	-	(6.0)
Number of snails per locality, average		68.0	152.5	520.6	627.7	
Number of species, slugs included		22	34	40	33	

TABLE 4

Mollusc occurrence in the herb-rich deciduous woods in relation to calcium (expressed as % of ash-free dry weight of the litter) and to some other environmental variables. The 24 localities have been rearranged into new Ca-poor and Ca-rich series (cf. Wäreborn 1969:476). The three locality groups in the table are based upon snail fauna similarities (ibid. p.477). Abbreviations: Loc. gr. = locality group; N.l. = number of localities; Mi = mean number of individuals (per locality with standard error, all the localities in the group are included). Exposure index (estimated): 1 = very shady, 5 = very exposed; mean values and intervals are presented. Significance (ordinary t-tests): 1) II/I, III p<0.10; 2) I/III p<0.05, II/I, III p<0.10; 3) I/III p<0.05; 4) I, II/III p<0.01; 5) I, II/III p<0.10; 6) I, II/III p<0.01 and 7) I/II p<0.05, I/III p<0.01.

Species	Ca-poor series		Ca-rich series		Loc. gr. I		Loc. gr. II		Loc. gr. III		Significance
	N.l.	Mi	N.l.	Mi	N.l.	Mi	N.l.	Mi	N.l.	Mi	
A) <i>O. alliarius</i>	5	1.2	2	0.2	3	0.9	2	1.0	2	0.2	
B) <i>V. ronneyensis</i>	-	-	-	-	-	-	-	-	-	-	
C) <i>V. substriata</i>	12	16.8	12	16.2	7	18.4±11.9	8	12.2±4.1	9	18.7±5.1	
<i>C. aspera</i>	12	7.5	11	19.9	7	10.8±4.1	8	20.0±6.9	8	10.3±5.0	
<i>E. fulvus</i>	12	39.9	12	48.4	7	25.8±8.6	8	58.6±14.3	9	45.5±18.0	
<i>N. hammonis</i>	12	44.4	12	76.8	7	44.1±6.1	8	96.8±22.9	9	41.3±9.9	1)
D) <i>D. rotundatus</i>	12	19.2	9	8.9	7	15.8±7.3	7	18.9±7.9	7	8.4±6.1	
<i>C. bidentata</i>	11	7.3	12	13.3	6	7.0±3.1	8	12.2±3.0	9	11.2±1.6	
<i>V. pellucida</i>	8	1.9	8	2.0	4	1.1	5	1.0	7	3.4	
<i>C. lubrica</i>	12	10.2	12	35.2	7	6.4±2.3	8	17.1±4.0	9	40.2±11.5	2)
<i>P. pygmaeum</i>	12	96.1	12	91.2	7	56.6±27.3	8	73.1±16.9	9	140.7±55.7	
<i>D. rudersatus</i>	9	7.2	9	3.2	4	4.4±2.9	7	4.5±1.5	7	6.6±2.7	
E) <i>A. pura</i>	7	15.6	4	4.3	7	26.7±9.0	4	6.4±3.1	-	-	3)
<i>V. crystallina</i>	8	22.7	2	8.4	6	19.0±7.9	2	9.8	2	18.1	
<i>C. laminata</i>	8	5.2	-	-	7	8.6±2.3	1	0.2	-	-	
<i>A. aculeata</i>	5	4.7	-	-	5	8.0±4.4	-	-	-	-	
<i>I. plicatula</i>	5	1.8	-	-	5	3.0±1.4	-	-	-	-	
<i>A. arbustorum</i>	7	0.8	2	0.0	6	1.3±0.5	1	0.0	2	0.0	
<i>C. edentula</i>	2	2.2	-	-	2	3.7±3.1	-	-	-	-	
<i>A. nitidula</i>	2	1.4	-	-	2	2.4±2.3	-	-	-	-	
F) <i>C. tridentatum</i>	9	66.2	7	185.8	5	33.8±16.2	5	55.0±27.0	6	260.8±136.3	
<i>N. petronella</i>	9	13.2	10	28.6	5	10.0±4.1	5	9.4±4.2	9	38.3±6.9	4)
<i>C. lubricella</i>	3	0.7	11	46.4	1	0.1	5	2.5±1.6	9	60.4±26.7	5)
<i>V. contracta</i>	3	1.6	9	7.0	1	0.6	3	1.2	8	9.9±2.4	6)
<i>B. fruticum</i>	-	-	7	1.9	-	-	3	0.8	4	1.9±1.3	
<i>T. hispidus</i>	1	0.0	2	10.5	-	-	1	0.0	2	14.0	
<i>V. alpestris</i>	-	-	2	0.3	-	-	-	-	2	0.4	
G) <i>V. pusilla</i>	6	1.7	8	2.9	1	1.0	6	3.9±1.8	6	1.9±0.7	
<i>C. hortensis</i>	7	0.3	11	2.4	5	0.3	6	2.6	7	1.1	
<i>H. lapicida</i>	4	0.7	6	1.1	3	1.1	3	0.6	4	0.0	
H) <i>V. excentrica</i>	-	-	4	0.1	-	-	1	0.0	3	0.1	
<i>V. pygmaea</i>	-	-	1	0.1	-	-	-	-	1	0.1	
Number of species (slugs included)	36		35		31		33		35		
Averages:											
Number of snails	387±87		614±115		311±67		407±84		730±152		
Ca, % in litter	18.7±0.6		30.8±2.2		18.0±0.8		29.3±3.8		25.9±2.0		7)
pH (under the litter)	5.9±0.2		6.3±0.3		6.1±0.3		6.0±0.3		6.2±0.3		
Soil moisture % (18.8.1966)	34.6±2.4		38.4±2.2		34.1±3.7		34.8±2.6		39.9±2.3		
Exposure index					2.1(1-3.5)		3.0(3-4.5)		2.4(1-4)		

Soil acidity is related to calcium content in the litter but not in a simple manner (Fig. 3). In localities with Ca between 14.0 and 16.0 %, pH values between 4.5 and 7.0 were found under the litter layer. Soils with humus of mor and moder type have mainly fungal decomposition and usually low pH values. In the litter of such habitats calcium occurs to a great extent as Ca oxalate. There are in the whole material positive correlations between species numbers and pH values (Fig. 4) and between abundance and pH (Fig. 5), but no such correlations were found in the separate series. In Tab. 3 there seems to be a decrease in species numbers at pH > 6.5. This agrees with findings in other areas (Ant 1963), but there were in this study only three localities in the pH class concerned.

RELATIONS BETWEEN INDIVIDUAL SPECIES AND ENVIRONMENTAL VARIABLES

In Tab. 4 the snail species were arranged into eight groups, A - F, according to their distribution in the five habitat series and to their relations to calcium in litter in the study area.

There is only one species in each of the two first groups (A and B). Oxychilus alliarius is partly a predator, occurring in all habitat series. Very few snails species are predacious; another case is mentioned below. The others mainly feed on dead plant material or/and on fungi and bacteria. Vertigo ronnebyensis is the only species, that was restricted to an oligotrophic locality series: it was found in the drier spruce forest.

In group C there are four species with high constancy in all series: Vertigo substriata, Columella aspera, Euconulus fulvus and Nesovitrea hammonis. The two latter species reach high abundances in the sun-exposed localities of group II. Furthermore, their abundance at seven herb-rich deciduous wood localities with light condition scores of 4 - 5 have been compared with nine, which have scores 1 - 2 (cf. Wäreborn 1969:472, 474). Mean numbers of individuals are for N.hammonis 101.6 at light localities and 35.2 at shady ones, $p < 0.05$. For E.fulvus the corresponding numbers are 63.6 and 25.8, $p < 0.05$.

Group D consists of six species, which to some extent occur in the three oligotrophic habitat series, but are much more abundant in the herb-rich deciduous woods: Discus rotundatus, Clausilia bidentata, Vitrina pellucida, Cochlicopa lubrica, Punctum pygmaeum and Discus ruderratus.

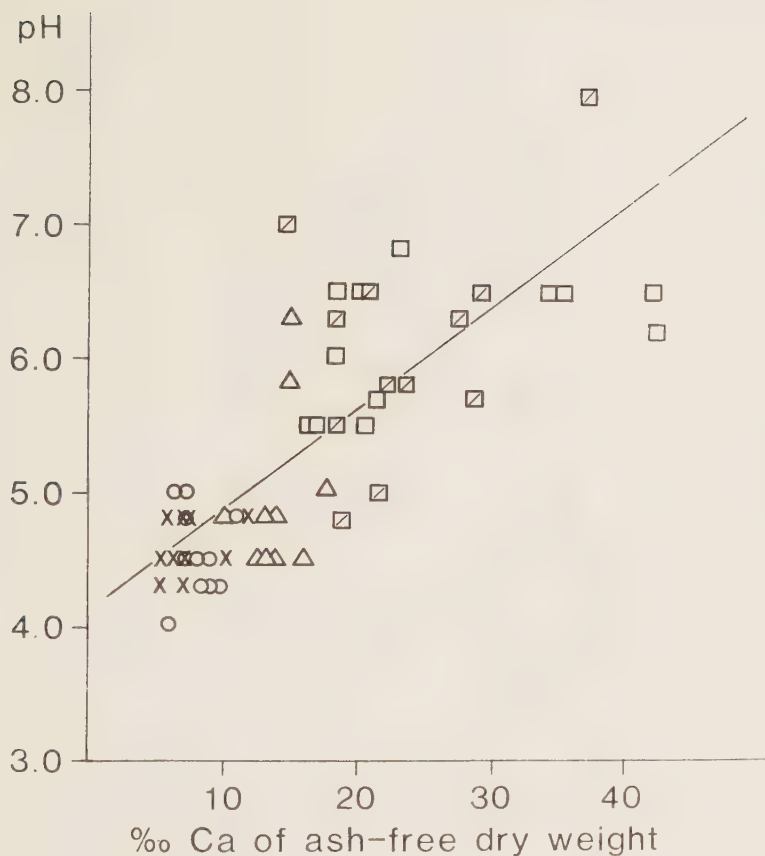


Fig. 3. pH value of the soil (measured under the litter layer) in relation to the calcium content of the litter (% Ca of ash-free dry weight, cf. Wäreborn 1969:465). X = the moist spruce forest locality series, O = the drier spruce forest series, Δ = the oligotrophic oak wood series, □ = the drier herb-rich deciduous wood series, and ⊠ = the moist herb-rich deciduous wood series. The correlation coefficient is 0.786, $p < 0.001$. Regression line $y = 0.0744x + 4.10$.

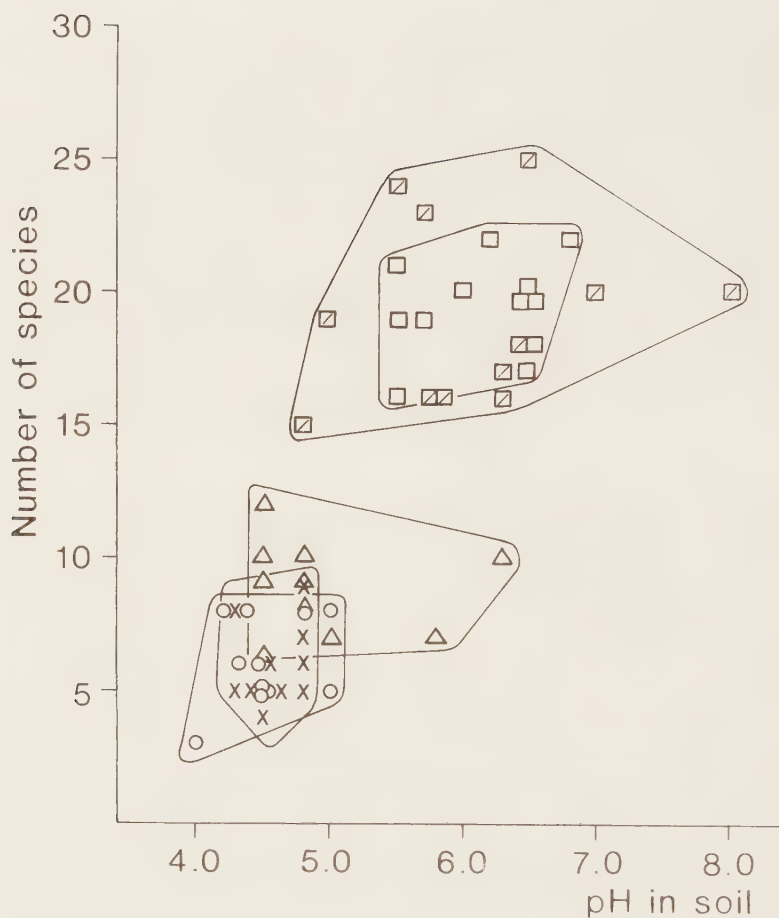


Fig. 1. Relations between the total number of mollusc species and the pH value of the soil (measured under the litter layer). X = the moist spruce forest locality series, O = the drier spruce forest series, Δ = the oligotrophic oak wood series, □ = the moist herb-rich deciduous wood series, and ▣ = the moist herb-rich deciduous wood series. There are no correlations between number of species and pH in the separate series, but totally these two variables are correlated: $r = 0.796$, $p < 0.001$, regression line (not drawn in the figure) $y = 5.77x - 18.31$.

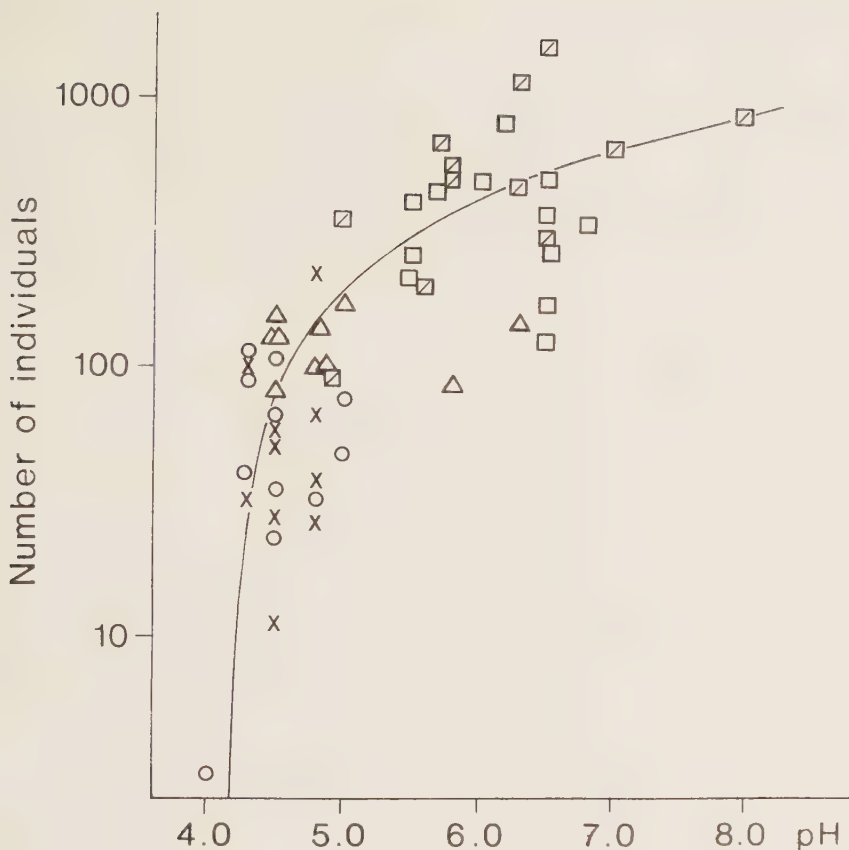


Fig. 5. Numbers of snails in relation to the pH value of the soil (measured under the litter layer). The numbers correspond to a sample of 3.0 l. x = the moist spruce forest locality series, O = the drier spruce forest series, Δ = the oligotrophic oak wood series, □ = the drier herb-rich deciduous wood series, and ◻ = the moist herb-rich deciduous wood series. There are no correlations between number of individuals and pH in the separate series, but totally these two variables are correlated ($r = 0.670$, $p < 0.001$, regression line $y = 232 x - 966$, the numbers of snails are in the figure given on a logarithmic scale).

Aegopinella pura, Mesovitrella hammonis and N. petronella: distribution between the locality groups (cf. Wärborn 1969:477); number of individuals/locality, recalculated to correspond to a sample volume of 3.0 l (ibid. p. 462).

Loc. No.	Loc. group I										Loc. group II						Loc. group III							
	33	39	49	37	67	10	13	12	31	70	30	32	68	9	34	16	47	42	45	44	41	40	38	35
A. pura	6	2	35	42	34	3	65	-	1	-	15	15	20	-	-	-	-	-	-	-	-	-	-	-
N. hammonis	45	64	57	45	36	14	48	70	196	26	125	182	38	85	52	29	52	57	31	111	27	33	18	14
N. petronella	-	25	21	-	6	1	17	-	-	5	22	21	-	+	27	44	13	9	41	21	71	54	53	30

Group E comprises six species, which in the study area mainly occur in the herb-rich deciduous woods and show a correlation with low calcium content in the litter: Aegopinella pura, Vitrea crystallina, Cochlodina laminata, Acanthinula aculeata, Iphigena plicatula and Arianta arbustorum. Two additional species with low constancy, Columella edentula and Aegopinella nitidula, seem to belong to this group. In the laboratory the latter species appeared to be partly predacious, attacking specimens of A.pura (cf. Frömning 1954); the soft parts and about half the shell were consumed.

In group F there are five species, probably correlated with high calcium content in litter, viz. Carychium tridentatum, Nesovitrea petronella, Cochlicopa lubricella, Vitrea contracta and Bradybaena fruticum. Two more species, which occur at a few localities but seem to be favoured by calcium, have been placed into this group, viz. Trichia hispida and Vertigo alpestris.

Group G consists of three species with a low abundance evenly spread over the three locality groups: Vertigo pusilla, Cepaea hortensis and Helicigona lapicida. Finally, group H comprises two meadow species, rarely occurring in woods: Vallonia excentrica and Vertigo pygmaea.

The rather closely related species Aegopinella pura, Nesovitrea hammonis and N.petronella were distributed in the herb-rich deciduous woods in a way that indicates interspecific interference (Tab. 5).

Slugs are difficult to sample quantitatively (cf. Wärebörn 1969:466). There were, however, discernible trends in their occurrence. Arion ater (L.), A.subfuscus (Drap.), A.silvaticus (Lohm.), Limax cinereoniger Wolf, L.marginatus Müll. and L.tenellus Müll. occurred in all series. At the localities of group I in the herb-rich deciduous wood only these species (except L.tenellus) were found. Arion circumscriptus Johnst. was found in group II and III and A.fasciatus (Nilss.), Deroceras agreste (L.) and D.laeve (Müll.) only in group III. The two latter species are common in other habitats than woods.

DISCUSSION

CALCIUM

Nearly all land-living molluscs might be favoured by calcium.

Possible exceptions are some slugs and the snail species Zonitoides excavatus (Alder) in Britain. The latter species is restricted to non-calcareous soils. It can, however, be reared on a mixture of oatmeal and chalk powder (Boycott 1934), i.e. its avoidance of calcium-rich habitats does not seem to depend directly on this element.

Calcium seems to be limiting for the snails in the three oligotrophic habitat series. It has been shown that deficiency of calcium restricts the reproductive output of Cochlicopa lubrica and Discus rotundatus in rearing experiments (paper C). Although the most Ca-rich localities in the herb-rich deciduous wood habitat had a much greater mean number of snails individuals per locality (Tab. 4), there is no general correlation in these woods between snail abundance and calcium or between species numbers of molluscs and calcium. A relatively small fraction of the total calcium is there bound as Ca oxalate. Easily soluble Ca salts predominate; they have a direct pH-increasing effect on the litter, and they are probably more directly accessible for the molluscs (cf. paper C). The mollusc species were in the herb-rich deciduous woods differently distributed in relation to calcium. The occurrence there of an assemblage of species (group E, see Tab. 4) correlated with low calcium content in the litter indicates effects of interspecific competition. Some of the species concerned occur elsewhere in very calcium-rich habitats (e.g. Cochlodina laminata, Aegopinella pura and Acanthinula aculeata on the island of Öland, Sweden).

SOIL ACIDITY

The pH values are related to differences in litter decomposition (mor, moder or mull type of humus), to calcium content and to chemical form of the existing calcium (cf. paper C). Specimens of some snail species reacted to pH differences in preference experiments (paper D). It was found in cultures of snails that the pH values per se may have an effect on reproduction at low pH and calcium levels (paper C). Correlations between mollusc distribution and pH values have been reported even from areas with calcareous bedrock (Cameron 1973).

Although the general picture of mollusc distribution in relation to soil acidity is similar everywhere (Peake 1978:479), the pH amplitude of a snail species may differ considerably in different geographical areas (cf. Økland 1930, Waldén 1955, Ant 1963,

Valovirta 1968, Wäreborn 1969, Bishop 1976, 1977). The differences in minimum pH values, stated by these authors, may be quoted here for some selected species: Acanthinula aculeata pH $\geq$ 4.5 - 6.1, Vitrea crystallina pH $\geq$ 3.9 - 5.5, V. contracta pH $\geq$ 3.9 - 5.0, Aegopinella pura pH $\geq$ 3.9 - 5.5, Cochlodina laminata pH 4.5 - 7.1 and Bradybaena fruticum pH $\geq$ 4.5 - 6.1. Various methods of measuring pH have been used; this has somewhat affected the results, but it cannot explain the differences. C. laminata seems to demand high pH values in England (Boycott 1934, Bishop 1976), while it occurs in rather acid deciduous woodland e.g. in Sweden and Germany (Waldén 1955, Ant 1963). Most species of a snail fauna are present at localities with very high pH, but in some of the species there is a moderate decrease in abundance also towards this end of the gradient (Valovirta 1968).

From this study one may infer that acidity-tolerant species accept low calcium content in the litter (Tab. 3). There should be differences between the species in ability to take up calcium. The calcium accumulated is probably partly used by the snails to neutralize the acid substratum, when they are creeping (paper D). They have a physiological system partly open to the environmental soil water, so they may need to defend themselves against hydrogen ions.

MOISTURE

Soil moisture plays an important role, which was particularly evident in the drier herb-rich wood series (Wäreborn 1969). The air humidity in the mollusc micro-habitats is also important. It depends upon soil moisture and exposition to sun and to wind (cf. Wäreborn 1969:465). Thick organic layers provide shelter from the dry air in the middle of the day and can give high minimum RH values even in localities with low soil moisture. Shady and cool localities have a high RH. Some species, e.g. Carychium tridentatum, are known to need near 100 % RH to be active (Morton 1955). The eggs of the molluscs develop in or under the litter. They are probably very sensitive to drought (cf. Ant 1963).

Nesovitrea hammonis, Euconulus fulvus and Columella aspera had high constancy in all series. Their abundance was almost as high in the oligotrophic oak wood as in the herb-rich deciduous wood. In the latter they reached highest abundance in the sun-exposed locality group II. The species mentioned all have a very wide

ecological amplitude in southern Sweden. They are not xerophilous (cf. Waldén 1969). Their increased abundance within locality group II may depend on decreased competition pressure there from drought-sensitive species (cf. Tab. 4 and Tab. 5). The litter of the oligotrophic oak woods is during droughts rather dry throughout, which may be a contributory cause of their relatively poor mollusc fauna.

COMPETITION

In the present study it is difficult to explain the existing pattern of occurrence without considering competition between species. Beside the examples above, the species Vitrea crystallina and V. contracta should be mentioned: out of 21 Vitrea localities in the two herb-rich deciduous wood series only one had both species (Wäreborn 1969:477, cf. Kuiper 1964). These observations in combination with the results of the preference tests (paper D) clearly indicate that interspecific competition occurs also in natural situations in critical periods of the year.

Ecological demands of a species may differ from one area to another. Differences in the pH amplitude are described above. Waldén (1966) gave an interesting survey of the habitat selection of Nesovitrea hammonis and N. petronella in various parts of Sweden. The former showed a slight but discernible tendency to prefer trophically favourable localities in the far north of Sweden. In southern Sweden it has a very wide ecological amplitude. With N. petronella the situation is reversed: it is widespread in the north but occurs mainly in moist and nutrient-rich wood habitats in southern Sweden.

Cochlicopa lubricella is in southern Germany a meadow species with some occurrence also in open, dry woods (Hagen 1952, Schmid 1966). In Sweden it occurs in open areas as well as in moist nutrient-rich deciduous woods. The species was in laboratory experiments shown to be affected by competition (paper D).

The mollusc populations may more or less differ genetically in various geographical areas. Two other possible explanations of the differences in autoecology described above may be given: 1) animals are able to compensate for adverse conditions in an area only in especially favourable habitats in this area; 2) there exist competitive equilibria, giving various results in different environments with different co-existing species.

The forests in the study area were little affected by human interference in comparison with conditions in Central Europe. The deciduous wood vegetation has, however, been cleared at many places, and spruces have been planted instead, which considerably affects the mollusc fauna. Land snails appear to be sensitive to acidification and calcium leaching (cf. paper C). Therefore they seem to be suitable objects for studies of effects of airborne pollution (cf. Waldén 1978, Ghilarov 1978).

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